THE COMPARATIVE ANATOMY OF THE HOMINOID CRANIAL BASE

by

Michael Christopher Dean

Thesis submitted for the degree of Doctor of Philosophy.

Department of Anatomy and Biology as Applied to Medicine, The Middlesex Hospital Medical School, University of London.

October 1982

VOLUME CONTAINS CLEAR OVERLAYS

OVERLAYS SCANNED SEPERATELY AND OVER THE RELEVANT PAGE.

ABSTRACT

This thesis uses metrical data and morphological observations to describe the comparative anatomy of the cranial base region in extant adult hominoids. The changes that occur during growth in this region have also been studied in samples of juvenile hominoids, and cross-sectional growth data for the same variables measured in the adult metrical study have been recorded. Detailed metrical and morphological observations were also made on a series of fossil hominid crania dating from the Plio-Pleistocene. The results of the two comparative studies of the cranial base region in extant hominoids were then used to assess the significance of the differences noted in the cranial base region of the fossil hominids from sites in South and East Africa.

The results of the adult metrical study; and the series of soft tissue dissections, demonstrate that there are fundamental differences in the comparative anatomy of the modern human and pongid cranial bases. The results of the comparative growth study indicate that these differences are probably not the result of an overall acceleration, or retardation, in growth rates of the component bones of the human cranial base, but more likely due to a combination of increases and decreases in growth rates occurring in individual bones, as well as to differences in morphology already manifest soon after birth. The results of the study of fossil hominid specimens indicate that the 'gracile' australopithecine fossils from South Africa have a cranial base pattern similar to that of the extant pongid samples, but that the 'robust' australopithecine fossils, and those fossils attributed to early Homo have a cranial base pattern more similar to the modern Homo sapiens sample.

These differences in basicranial anatomy among the fossil hominid sample provide a useful tool to assess the taxonomic status of several

hominid fossil specimens which are still of uncertain taxonomic designation. The comparative studies of the hominoid cranial base also provide a framework which enables features of this region to be used in phylogenetic analysis.

ACKNOWLEDGMENTS.

I would first like to thank my Supervisor, Dr. Bernard Wood, for his wise and patient supervision and for his kindness and friendship towards me during the last five years.

Much of the work in this thesis was carried out in the Department of Anatomy, The Middlesex Hospital Medical School, Cleveland Street, London, W.C. 1 and I would like to thank Professor P.H. Silver for his generosity in making facilities available to me, even after the termination of my studentship. I would also like to thank Mr. A. Rote and Mr. S, Karby for their help with the preparation of many wet specimens and Mr. C. Sym for his invaluable help with the photography.

I am also very grateful to Dr. Michael Clarke for his generous help with computing problems.

During the past five years many people have given me practical help and encouragement and I would like especially to thank the following: Ms. S. Abbott, Professor A. Boyde, Professor G.H. DeBoulay, Mr. T. Bryant, Mr. M. Catchpole, Mrs. M.J. Harvey, Dr. P.N. Holmes and Mr. A. Hughes.

I would also especially like to thank the following trustees of many museums for their assistance and stimulating interest in my work and for allowing me access to valuable collections of extant primate and fossil material: Dr. C.K. Brain and Dr. E.S. Vrba, Professor P.V. Tobias, R.E.F. Leakey and M.D. Leakey, Mrs. P. Napier and C. Powell-Cotton, L.R. Barton and M. Harman.

I am also extremely grateful to Elizabeth Marshall and Janet Marx for typing the figures and manuscript.

This thesis was supported by an N.E.R.C. Research Studentship.

TABLE of CONTENTS.

LIST of TABLES.

LIST of FIGURES.

Page.

LIST of PLATES.

INTRODUCTION.

Since the publication of Charles Darwin's 'Origin of Species' in 1859, structural links between the base of the cranium of modern man and non-human higher primates have often been cited as evidence for the evolution of man. However, in the years following the publication of Darwin's 'Origin', the steady accumulation of fossil evidence has tended to direct attention away from the cranial base and towards the study of the neurocranium, facial skeleton, dentition and postcranial elements of the skeleton. Thus, in the last few decades it is changes in these areas which have preoccupied hominid paleontologists.

This present thesis arose from the realization that sufficient numbers of fossil hominid crania have now been recovered to warrant a reappraisal of the evolutionary changes in the morphology of the cranial base. This new evidence also provided the opportunity to review the potential importance of cranial base anatomy for the interpretation of hominid phylogeny. It was soon apparent that while there is marked variation among the basicranium of early fossil hominids, any attempt to assess the significance of these differences required a comprehensive metrical and morphological study of the cranial base region in both extant primates as well as the fossils themselves.

The work presented in this thesis relates to four separate, but interrelated, research problems. The first was to establish a metrical framework which could be used to examine the extent of any differences in the size and shape of the cranial base among the samples of extant hominoids chosen for this study (Homo sapiens, Pan troglodytes, Pongo pygmaeus and Gorilla gorilla). The second was to document the major postnatal ontogenetic changes that occur in the hominoid basicranium, and explore the use of these changes in the basicranium as a model for interpreting changes seen during hominid evolution. The third was to try to relate the osteology

of the cranial base to what is known of the soft tissue anatomy. Lastly, the results of the preceding three studies were to be used to document and interpret any consistent patterns and trends in the basicranial anatomy of fossil hominids.

The majority of previous studies of the cranial base have tended to concentrate upon midline structures. In this thesis particular emphasis was laid on anatomical features lateral to the midline, and most of the measurements were made with the cranial base viewed in norma basilaris.

The plan of this thesis is that the first part is devoted to a review of the literature dealing with the comparative anatomy of the cranial base. This part is itself divided into four sections. These in turn deal with the comparative anatomy of the adult hominoid basicranium; postnatal growth changes in the cranial base of hominoids; the soft tissue anatomy associated with the cranial base, and the literature dealing with the basicranial morphology of fossil hominids.

The second part of this thesis describes the materials chosen and the methods used, and the third part the results obtained for each of the four research studies outlined above.

The fourth part is a discussion section in which the results are assessed in the light of previous studies of cranial base anatomy, and in the same section the implications of these results for hominid phylogeny are evaluated.

The literature cited is set out in part five and a concluding appendix section, part six, sets out the data obtained during the study, and also includes lists of specimens which make up the comparative samples.

PART I LITERATURE REVIEW

Chapter 1. The basicranium of adult hominoids and related studies.

Chapter 2. Growth changes in the cranial base of hominoids.

Chapter 3. The soft tissues associated with the hominoid basicranium.

Chapter 4. The cranial base of fossil hominids.

CHAPTER 1.

The basicranium of adult hominoids and related studies.

Detailed anatomical descriptions of the cranial base have appeared in the anatomical literature from the earliest times, and many well known anatomists such as Vesalias (1514-1564) and Morgagni (1682-1771) were among the first associated with its study. It was, however, not until the middle of the nineteenth century, with the publication of Darwin's 'The Origin of Species' in November 1859, that anatomists concerned with this area found themselves at the centre of the bitter arguments which took place in order to establish the principles of natural selection that Darwin had so cogently laid down. Some anatomists, such as the comparative anatomist Richard Owen, became ardent critics of Darwin, yet others were among the first to be convinced by the arguments for biological evolution. Thomas Huxley, one of Darwin's strongest supporters, was convinced about evolution, but also believed that natural selection as the primary mechanism of evolutionary change had not yet been subjected to experimental proof. It was, however, through Huxley's vigorous defence of Darwin, and by his efforts to accumulate evidence for Darwin's ideas, that the anatomy of the cranial base came to figure so prominently in these evolutionary arguments. Huxley's essays 'Evidence as to man's place in nature' published in 1863, contain the earliest and clearest accounts of the cranial base in this new context. Huxley (1863, p. 148, second paragraph) writes,

> "I have arrived at the conviction that no comparison of crania is worth very much, that is not founded upon the establishment of a fixed base line, to which the measurements, in all cases, must be referred. Nor do I think it is a very difficult matter to decide what that base line should be. The parts of the skull, like those of the rest of the animal framework, are developed in succession; the base of the skull is

formed before its sides and roof; it is converted into cartilage earlier and more completely than the sides and roof: and the cartilaginous base ossifies and becomes soldered into one piece long before the roof. I conceive then that the base of the skull may be demonstrated developmentally to be its relatively fixed part, the roof and sides being relatively moveable. The same truth is exemplified by study of the modifications which the skull undergoes in ascending from the lower animals up to man."

Huxley (1863, p. 148) defined the 'basicranial axis' as "a line drawn through the bones termed basioccipital, basisphenoid and presphenoid" and in a subsequent publication, Huxley (1867, p.67) as "a line drawn through the middle vertical plane of the basioccipital - basisphenoid and presphenoid from the hinder extremity of the former bone to the anterior extremity of the last, at the upper end of the ethmo-presphenoid suture". Huxley (1863. p.150) defined the angle between the 'basicranial axis' and the plane of the foramen magnum in the midline as the 'occipital angle', the angle between the 'basicranial axis' and the "plane of the perforated plate by which the filaments of the olfactory nerve leave the skull" as the 'olfactory angle' and the angle made by the basicranial axis with the facial axis as the 'cranio-facial angle'. These angles are now more usually referred to as the foraminobasal, the spheno-ethmoidal and the spheno-maxillary angles.

Huxley (1863, p.150, second paragraph) continues,

"But if a series of sections of mammalian skulls intermediate between a rodent and a man, be examined, (see Figure 1), it will be found that in the higher crania the basicranial axis becomes shorter relatively to the cerebral length; that the 'olfactory angle' and 'occipital angle' become more obtuse; and that the 'cranio-facial angle' becomes more acute by the sending down, as it were, of the facial axis upon the cranial axis. So that, at last, in the human skull, the cerebral length is between

FIGURE 1.

Taken from Huxley, T.H., 1863, p. 149

> twice and thrice as great as the length of the basicranial axis; the olfactory plane is 20^{o} or 30^{o} on the under side of that axis; the occipital angle, instead of being less than 90^{o} is as much as 150^{o} or 160^{o}; the cranio-facial angle may be 90^{o} or less, and the vertical height of the skull may have a large proportion of its length.
>
> It will be obvious that the basicranial axis is, in the ascending series of Mammalia, a relatively fixed line, on which the bones of the sides and roof of the cranial cavity, and of the face, may be said to revolve downwards and forwards or backwards, according to their position .....
>
> Now comes the important question, can we discern, between the lowest and the highest forms of the human cranium anything answering, in however slight a degree, to this revolution of the side and roof bones of the skull upon the basicranial axis observed upon so great a scale in the mammalian series ? Numerous observations lead me to believe that we must answer this question in the affirmative."

Huxley goes on to demonstrate that the more prognathous Australian and Negro skulls have smaller occipital angles than the skulls of a Tartar and an individual from Constantinople but adds that the more prognathous skulls are "less ape-like" in that the "cerebral cavity projected decidedly more beyond the anterior end of the axis" (see Figure 2). Huxley (1867) later presented a detailed description of two widely contrasted forms of human crania, thus extending his earlier observations about modern human crania.

These early studies of Huxley's formed the basis of most of the work carried out on the adult cranial base of modern man and the higher primates during the nineteenth century. Aeby (1867), however, disagreed with Huxley's interpretation that the slope of the foramen magnum was related to the basicranial axis and the degree of prognathism. Instead, he saw it as being connected with the degree of development of the occipital region. Keith (1910) also took the view that growth of the nuchal planum had much to do with the orientation of the foraminobasal angle. However, Bolk (1910,

FIGURE 2.

co
pl
en

Taken from Huxley, T.H., 1863, p.151

p.529) pointed out that Aeby's interpretation did not differ fundamentally from Huxley's and added that "a slight shortening of the clivus is of great influence on the angle of the slope". He also commented that the slope of the foramen magnum is in any case very variable, especially in the anthropoidea. Bolk was critical of defining the position and inclination of the foramen magnum from the basicranial axis, which was itself so intimately associated with the foramen magnum. Bolk (1909) devised a "basal index" to measure the position of the foramen magnum in man and the primates. This expressed the length of the preoccipital part of the cranial base in terms of the length of the whole of the cranium. Thus, the more posterior the position of the basion, the greater the numerical value of the index. Bolk (1910) showed that the foramen magnum was more anteriorly situated in man than in the great apes and went on to demonstrate that the slope of the foramen magnum increased (i.e. became more vertical) in crania in which it was more posteriorly placed. Bolk believed that these changes in the cranial base were due to changes that had occurred in the growth of the brain, a view that Weidenreich (1941) was to adopt later in the century.

Duckworth (1904, 1915) re-emphasised the importance of the cranial base region as a key to understanding the changes in cranial morphology which have occurred during human evolution. He drew attention to the gradual decrease in the size of the spheno-ethmoidal angle from the lower mammals to man; such an angle, he ventured, "gives a good indication of the gradual increase in the development of the frontal lobes of the brain".

Young (1916) made observations on a large collection of some 700 Scottish skulls obtained from a Glasgow burial ground in use up until about 1840. Young concluded (as Huxley (1867) had done) that there was no relationship between the total length, or the degree of flexion, of the cranial base, and cranial capacity. Young demonstrated that in a series of 98 skulls from this collection, the spheno-ethmoidal angle varied from 137^{o} to

170°, with a mean value of 152°. He noted that the higher values for this angle were greater than those given for the gorilla and chimpanzee, but could find no reasonable explanation for this, except to question the use of this angle in comparisons between the human and non-human primates.

Cameron, in a remarkable series of forty papers published between 1924 and 1932 (see Ruch (1941) for a full bibliography), investigated angles and indices of the cranial base in races of man, and in other higher primates. Some of Cameron's papers are particularly important. Cameron (1924, 1925) suggested that the point which Huxley called prosphenion was not the site at which cranial base flexion occurred during prenatal growth of the human skull. Instead, he claimed that the 'pituitary point' (the anterior edge of the groove for the optic chiasma in the midline) was probably the site of flexion of the anterior part of the skull base. Cameron (1927) devised the 'main angle of cranial base flexion' (the nasion-pituitary point-basion angle), and demonstrated that this angle was greatest (i.e. least flexed) in the Negro races of modern man. In addition Cameron (1926, a and b) demonstrated that nasion-basion length showed racial variation, being greatest in the Negro and shorter in White races. However, when he looked at the anterior part of the skull base alone (i.e. from nasion to the pituitary point) this part was longest in the White races. Cameron (1930, p.329), in a review of his own work on the angle of cranial base flexion, noted that he "was candidly astonished to find" that the skull of Tarsius possessed a well marked degree of skull base flexion (151°), nearer than any other primate to the value of 135° for the Negro cranium. This finding was to be an important one for, according to Cameron, it was additional evidence to that already put forward by Wood Jones to suggest that Tarsius occupied a higher position on the evolutionary scale than the one usually accorded it (Wood Jones, 1929 a and b). The cranial base had thus become established as an important anatomical area in the study of primate evolutionary biology.

During the second decade of this century anatomists were beginning to turn their attention to basicranial structures other than those in the midline. Wood Jones (1923) drew attention to the fact that the pattern of articulation of the frontal, ethmoid and sphenoid bones in the floor of the anterior cranial fossa varied considerably in primates. This, and other evidence including observations about soft tissue anatomy, led Wood Jones to believe that these different structural arrangements indicated different principles of growth, and a greater degree of divergence between man and the non-human primates than was suggested by the many more superficial likenesses they shared. The articular patterns of the anterior cranial fossa in modern man were first noted in detail by Le Double (1903), who proposed a "classification of human variations" based upon variations observed in the skull of man and other lower animals. In modern man the sphenoid bone usually articulates with the posterior part of the ethmoid bone; Wood Jones noted that in the pongids and Old World Monkeys the frontal bone intervened between these two bones, preventing a spheno-ethmoidal articulation in the anterior cranial fossa. Gregory (1927) challenged Wood Jones's interpretation and asserted that the pattern in both modern man and the non-human primates was basically the same. Ashley Montagu (1943) recorded the incidence of a spheno-ethmoidal articulation in Pongo as 100%, Pan as 85%, Gorilla as 47% and in Hylobates, 0% (the remaining animals showing the frontal bone intervening between the sphenoid and ethmoid). Butler (1949) reported the incidence of the 'retro-ethmoid frontal suture' in the anterior cranial fossa as 24% in a series of twenty-five human skulls from Bengal, but observed no correlation with sex, age or cephalic or gnathic index. Murphy (1955), in a much larger series of 453 human skulls, described seven types of spheno-ethmoidal articulation in the Australian aborigine alone, and in only 8% of the skulls did he find the frontal bone intervening between the sphenoid and ethmoid. These later studies thus emphasize that substantial intraspecific variation in the anatomy of this region, in both man and the non-human primates,

reduces the taxonomic importance of the differences referred to by Wood Jones. Gregory (1952) has pointed out that the retro-ethmoidal frontal suture is a "superficial thing overlying the primary cartilaginous joint union of the sphenoid and ethmoid, developing in the adult as a structural readjustment during growth of the orbits". However, the importance of these earlier studies lies in the fact that when there is a spheno-ethmoidal articulation, the length of the ethmoid bone in the anterior cranial fossa is a true reflection of its total length. This is not the case when the frontal bone intervenes between the sphenoid and ethmoid, and in these cases the total length of the ethmoid can only be measured from sagitally sectioned skulls or from good quality lateral skull radiographs.

Schulter has since extended these earlier observations about racial variation in the cranial base of modern man by making a detailed study of the temporal bone. Schulter (1976) made a comparative study of the temporal bone in three modern human populations using radiographs taken in two planes (norma lateralis and norma verticalis) supplemented by measurements taken directly from the skulls. This is one of the few studies of the cranial base in which linear and angular measurements have been recorded lateral to the midline with the skull orientated in norma verticalis as well as in the sagittal plane. Schulter describes three angles which record the angulation of the tympanic and petrous parts of the temporal bone to the midline, the petrosagittal, petrosquamous and petrotympanic angles. He also records differences in the nasion-sella-basion angle (almost identical to Cameron's angle of cranial base flexion) measured in the sagittal plane. Schulter defines the petrosagittal angle as the angle formed by the midline of the skull base (passing through nasion, basion and opisithion)and the petrous axis (represented by a line joining the centre of the stylomastoid foramen and the lateral margin of the spheno-occipital synchondrosis). He defines the petrotympanic angle as the angle formed by the petrous axis and "a line drawn through the length of the tympanic

plate where it forms the anterior wall of the external auditory canal".

These definitions of the petrous and tympanic axes differ from those of Weidenreich (1943, p.57, see Chapter 4), who states that "the vertex of the angle formed by the petrous and tympanic axes coincides with the carotid foramen". Thus Weidenreich uses a line joining the apex of the petrous pyramid and the carotid canal to represent the petrous axis, and a line joining the carotid canal and "the transverse axis of the tympanic plate" to represent the tympanic axis. Both Schulter and Weidenreich measured the angulation of the petrous axis relative to the midline of the skull base, thus larger values for this angle represent a petrous axis orientated more horizontally across the skull base and smaller values, a petrous axis orientated so that it is inclined more towards the sagittal plane. Schulter found that the mean value for the petrosagittal angle for 98 White skulls was 52.6^{o}, whereas Weidenreich quotes a value of 63^{o} for one European cranium. The smallest mean value of the petrosagittal angle in Schulter's study occurs in the sample of 98 Eskimo crania (49.5^{o}). Interestingly, this racial group also has the highest mean value for the cranial base deflection angle (nasion-sella-basion) in the study. In other words, more forward pointing petrous axes are associated with a skull base that is less flexed in the midsagittal plane. The differences in petrosagittal angulation between the three racial subsamples are, however, small in Schulter's study (Eskimos 49.5^{o}, Indians 51.6^{o}, Whites 52.6^{o}) and are less marked than the differences in the mean values of cranial base flexion (Eskimos 135.3^{o}, Indians 130.9^{o}, Whites 128.2^{o}).

Schulter concluded that "as the petrosagittal angle 'opens', the petrous pyramid (particularly its lateral aspect) moves forward, and the medial portion of the tympanic plate may be dragged forward with this movement. The lateral portion of the plate should not move because of the strong root of the zygoma coupled with a need for an adequate mandibular

fossa". None of the angles measured by Schulter showed any variation between sexes and correlations between the various angles are very low, something which Schulter interprets as evidence for the 'stability' of the cranial base. Schöneman (1906) undertook a less exhaustive investigation of the relationship between the cranial base and the temporal bones earlier this century, and concluded that the temporal bones were an important determining factor in the overall morphological pattern of the skull.

The majority of more recent studies of the cranial base of adult hominoids have been concerned with the functional interrelationships between the component bones. The discovery of well preserved fossil hominid crania has drawn attention to the potential value of the cranial base in helping to interpret the posture and locomotion of extinct forms. The literature dealing with studies such as these is best reviewed in two sections. The first will deal with functionally orientated studies of the cranial base, and the second will consider the literature which deals with allometric changes, and studies which have tried to relate foramen magnum and occipital condyle position and orientation with posture and locomotion.

Studies have shown that differences of size and shape in skulls are due to the functional remodelling of the neuro- and viscerocranium during the growth period. DuBrul and Laskin (1961) removed the spheno-occipital synchondrosis from growing rats and demonstrated that, as a result, marked changes in the shape of the skull occurred. These changes included a midline kyphosis and an inward rotation of the petrous pyramids towards the midline. These same changes were noted by Bateman (1954) while studying the effects of grey lethal and micro-ophthalmic gene mutations in mice. Koski (1968) has suggested that observations such as these "do not prove that the cartilage of the spheno-occipital synchondrosis has an independent growth-promoting potential", and that growth there may only be a response to external stimuli. When the spheno-occipital

synchondrosis is transplanted to a relatively nonfunctional site (Baer, 1954), the pattern of growth is not the same as than seen in situ. The cartilage appears not to have the same amount of independent growth potential as that observed in transplants of epiphysial cartilage under the same experimental conditions (Koskinen and Koski, 1967 and Rönning, 1966). Koski notes that there is comparatively little postnatal growth at the spheno-occipital synchondrosis in man, and claims that there is no direct evidence to support the view that the spheno-occipital synchondrosis is an important growth centre for the craniofacial skeleton. Moss (1975) has demonstrated that changes similar to those observed by DuBrul and Laskin and Bateman could also occur as a result of interfering with normal function during growth. Moss has contributed extensively to the literature dealing with the functional interrelationships of skeletal and soft tissues, and this will be referred to again in Chapter 3. However, several studies concerned specifically with differences in adult skulls will be reviewed here.

Moss and Young (1960) have demonstrated their functional approach to craniology in several ways. They hypothesize that growth of the brain is 'tied down' by organised tracts of fibrous dura mater to the originally cartilagenous cranial base at five points. These are the crista galli in the midline, and the lesser wings of the sphenoid and petrous crests of the temporal bone more laterally. This arrangement allows expansive growth in certain directions only, and factors such as binding of the infant head can act, through the connections of the dura mater, to produce malformations of the cranial base. Moss (1958) describes two types of cranial deformation resulting from binding of the head in North and South American Indians. The 'vertical' type includes those cases in which the plane of the occipital squama is vertical with respect to the face and an 'oblique' type where the occipital squama is orientated obliquely backwards with respect to the face. Moss demonstrated that posterior compression in 'vertical' deformation compressed the clivoforaminal angle and elevated

the lateral part of the petrous crest, while the reverse occurs in 'oblique' compression. McNeill and Newton (1965) were not, however, able to demonstrate any relationship between vault deformation and modifications of the cranial base. Moss (1958) noted that the basilar part of the occipital bone moves as a unit, rotation of the clivus in either direction being apparently accompanied by a corresponding rotation of the foramen magnum "as if both basion and opisthion are rotating about a common center in the posterior clinoid region of the sella".

Moss (1963) investigated the 'clubbing' of the crista galli of the ethmoid and came to the conclusion that it was the result of increased tension in the dura resulting from the rotation of the neurocranium and falx cerebi. He claimed that marked 'clubbing' of the crista galli and rotation of the cranium were associated with depression of the petrous crests to which the tentorium cerebelli attaches.

Bull (1969) has argued that the functional role of the dural tracts has changed during mammalian evolution. In birds and lower mammals the tentorium cerebelli forms a fibrous separating membrane, and the weight of the brain being trivial, is supported by the flat floor of the cranial base. In man, following the massive increase in size and weight of the brain and the rotation of the foramen magnum through 90^{o}, the tentorium cerebelli acts as a support against gravity to prevent the brain herniating through the foramen magnum. Thus, by virtue of its increased area, the greater sagittal angle of its inclination, and by being divided into two angulated planes, the tentorium cerebelli transmits the weight of the occipital lobes of the brain outwards towards the rigid bony skull.

Moss and Young (1960) point out that the overall spatial relationship of soft tissue structures have a profound bearing on the bony architecture of the skull. It is, they claim, the very different relationships between the orbit and the brain which result in a large supra-orbital torus in the gorilla, but a much smaller one in the orang utan or man, where the brain lies more

anteriorly over the orbits. Weidenreich (1941) claimed a similar pattern of relationships in the dog. Although this particular argument does not affect the cranial base, it is important when the spatial relationships of the facial skeleton to the skull base are considered.

Studies which relate cranial base anatomy to posture form an important section of the literature. Many authors have drawn attention to the fact that the foramen magnum and occipital condyles in the human are situated relatively further forward than in other extant primates, e.g. Bolk (1909), Senyurek (1938), Schultz (1955), Ashton and Zuckerman (1956) and Le Gros Clark (1971). Several investigators, including Beigert (1957, 1963), Du-Brul and Laskin (1961) and Le Gros Clark (1971), have linked this with flexion of the skull base. With the exception of Beigert, all these authors maintain that the degree of basicranial flexion and the position of the foramen magnum and occipital condyles are posture related. Beigert, however, regards increased flexion of the skull base as a phenomenon mainly concerned with an evolutionary enlargement of the neopallium and with a reduction in the relative size of the masticatory apparatus. He considers that the cranial base is more influenced by changes in the craniofacial region and by interspecific differences in the masticatory apparatus than they are by posture. Thus, primates with larger bodies often have a larger masticatory system relative to brain size than small primates. The corollary is that when brain size is relatively large, the position of the occipital condyles would be more forward, and Beigert claimed that because of this relationship, condyle position is not a good criterion for determining the degree of upright posture. However, if this is the case, then the prediction would be that because of the positive allometry of the jaw apparatus and the negative allometry of brain size, small animals would be expected to have a 'large' brain when 'expressed' in terms of jaw size. In such animals, such as the squirrel monkey, Beigert did indeed find that the occipital condyles are situated more anteriorly in the cranial base.

Moore, Adams and Lavelle (1973) suggested that a reliable indication of head poise would be provided by the angle at which the vertebral column approaches the skull, and that this can be estimated by the angles at which the condyles are set on the cranial base. In a later paper Adams and Moore (1975) claim that "if a horizontal plane of the head, as held in its habitual posture, can be defined, then the angle at which the spine approaches that plane will define the angle at which the spine is habitually held relative to the ground, i.e. it will indicate general bodily posture". Downs (1952) found that in 100 orthodontic patients the Frankfurt Horizontal varied from the true postural horizontal, as determined when an individual was looking into his own eyes in a mirror, by an average of only 0.9^{o}. Moore et al (1973) measured the angle between a perpendicular to the anteroposterior plane of the left condyle (i.e. an estimate of the line of the vertebral column) and the Frankfurt Horizontal in Homo sapiens, Gorilla, Pan and Pongo as well as casts of certain fossil hominids. The angle in man was close to 90^{o} and underwent little change with age. In the adult apes, the angle ranged between 53^{o} and 67^{o} and underwent a reduction of nearly 20^{o} during development. These data, so the authors claim, correlate with the upright posture of man from a very early age, and the change fron brachiation in juvenile apes to the 'knuckle walking' adult apes. However, the finding of a relatively low value for the angle in adult Pongo - a brachiator - runs counter to the thesis that the angle is a direct reflection of overall posture, and thus casts some doubt on the conclusion that the large values of this angle in certain australopithecine fossil casts measured by the authors necessarily indicates that these creatures stood upright. Cramer (1977) in an account of the craniofacial morphology of Pan troglodytes and Pan paniscus has shown that the occipital condyles and foramen magnum are relatively further forward in Pan paniscus than they are in Pan troglodytes. This difference is also associated with an increased degree of cranial base flexion even though the habitual posture is the same in the two animals. Cramer also

paniscus draws attention to the fact that "multiple regression analysis, utilizing the cranial base angle as the dependent variable, indicates that at least 40% of the variance between the two species can be accounted for on the basis of craniofacial variables alone". Huxley (1863) had, long ago, assumed a relationship between the degree of prognathism and the skull base and Björk (1950) in this classic paper on the biological aspects of prognathism outlined several features of the facial skeleton and cranial base that he considered to be interrelated. Björk considered that differences in facial prognathism among animals, or between different human races, were mostly due to differences in the size of the jaws. He considered the increase of the cranial base angle and rearward displacement of the foramen magnum during the growth period in anthropoids as a "compensatory development, necessary in order to counteract the pronounced increase in jaw length". Björk studied the relationship between mandibular prognathism and flexion of the cranial base in the crania of 281 Swedes and 238 Bantus and concluded that within the individual ethnic groups an increase in skull base flexion, or a shortening of the skull base, was related to increased mandibular prognathism. Later Scott (1953, 1958) also suggested that there was a relationship between cranial base morphology and facial prognathism. Quoting data from Young (1917) for the length of the skull base (basion to nasion) and the basion-alveolare length (Scott, 1953), and in a later paper for the sphenomaxillary and spheno-ethmoidal angles (Scott, 1958), he claimed that there was "a general but not exact correlation between cranial flexion and facial prognathism". He drew attention to the fact that the pronounced facial prognathism of the baboon is associated with a cranial base angle of 148^{o}, a value which is nearer to the mean modern human value of 133^{o} than that of any other higher primate. Scott (1954, 1958) has also drawn attention to the importance of the function and position of the nose as a part of the facial skeleton, and suggests that a diminution in the size of the nose due

to a reduction in its function as an organ of heat loss may account, in part, for the decrease in size in the face of modern man.

The relationship of the facial skeleton to the skull base is complicated, but there are clear indications from published research on extant taxa that modifications in the viscerocranium are associated with marked changes in the basicranium. This review of the literature concerned with the adult hominoid skull base illustrates very well the trend away from purely descriptive studies of the adult cranial base towards research that suggests a more complicated view of the basicranium as the functional interface between the facial skeleton, the neurocranium and the vertebral column.

CHAPTER 2.

Growth changes in the cranial base of hominoids.

The idea of there being parallels between phylogeny and ontogeny was put forward by Aristotle and then propounded much later by William Harvey in 1645, and again by Meckel (1811) and Serres (1824) who reiterated the view (see de Beer 1962, Wind 1970 and Gould 1972 for a comprehensive historical review). The view of Meckel and Serres that during ontogeny an individual actually passed through the adult forms of lower animals was discredited by Von Baer (1828). Von Baer objected to this theory on the grounds that development proceeds from the general to the special, the earliest embryonic stages of related organisms being nearly identical with distinguishing features added later as heterogeneity differentiates from homogeneity. Thus, Von Baer concluded that 'true' recapitulation is impossible, and instead put forward the theory that young embryos are undifferentiated general forms, not previous adult forms. Despite these objections, in 1866 Haeckel published his famous 'biogenetic law' stating that "ontogeny is the short and rapid recapitulation of phylogeny ..... during its own rapid development ..... an individual repeats the most important changes in form evolved by its ancestors during their long and slow palaeontological development", and later added that "phylogenesis is the mechanical cause of ontogenesis" (Gould 1977, p.77 and p.78). Phylogeny to Haeckel meant the "chain of manifold animal forms that represent the ancestry of an organism, i.e. the phyletic line of succession of adults" (see Wind 1970, p.8). The theory of recapitulation had great impact and formed a powerful framework for biological exploration during the latter half of the nineteenth century. Gould (1977, p.77) quotes Haeckel as regarding his law as "the thread of Ariadne", stating that "only with its aid can we find any intelligible course through this complicated labyrinth of forms".

The influence of Haeckel's law is still apparent in the relatively recent anthropological literature. Wood Jones (1929) writing about man's origins among the tarsioids, argued that the early ontogenetic fusion of the maxillary-premaxillary suture in man precluded an origin from the monkeys and apes (and even from the australopithecines). Considering the fusion of these two bones Wood Jones deemed it "probable that its early ontogenetic accomplishment is a guarantee of its early phylogenetic acquirement" (1929, p.319). Groth (1937) in a discussion of the mastoid process, relates the late appearance of this structure in man's ontogeny to its late appearance in his phylogeny and Negus (1949) also implies that there are parallelisms in the ontogeny and phylogeny of the human larynx. Le Gros Clark (1971, p.270) notes with interest that the human embryo has four endoturbinals, implying that this is evidence for a reduction in the turbinal system sometime during the evolution of man. A relationship between ontogeny and phylogeny was widely acknowledged and generated a degree of expectation among biologists and comparative anatomists such that Cameron (1930, p.39), see Chapter 1, "was candidly astonished" to find that the skull of Tarsius presented a well marked degree of skull base flexion (151^{o}), nearer to the value of 135^{o} for the Negro cranium than any other primate !

Nevertheless, by the end of the 1920s the theory of recapitulation had fallen into disrepute and anthropologists were beginning to interpret human evolution in precisely the opposite manner. The theory of recapitulation contained a fatal flaw. If the adult traits of ancestors become juvenile features of descendants, then development must be speeded up to make room for the addition of new adult characters onto the end of a descendant's ontogeny. Thus the "law of acceleration" gave way to the "law of retardation". Louis Bolk (1866-1930) led the movement that argued that human beings had evolved by retaining the features of the juvenile stages of their ancestors, while gradually losing the distinctive characteristics of adult anthropoids.

Weidenreich (1941, p.410) later pointed out that "the ape fetus shows a more human aspect not because the apes are desendants of a more human-like ancestor as a consequent application of Haeckel's biogenetic law would suggest, but because man preserves the fetal type until the end of his growth". Characters which are present during the development of an ancestral animal may appear in the adult form of a descendant as a result of a relative retardation of the growth process. This process is known as neoteny or paedomorphosis. Bolk (1926) refers to this process as foetalization and cites the degree of cranial base flexion and the failure of the human spheno-ethmoidal angle to open out during ontogeny as examples supporting his view that man evolved by retaining the juvenile features of his ancestors. Bolk summarized his theory in one sentence; "Man represents a fetus of a primate that has become mature".

This view gained wide acceptance but Gould (1977) points out that the traditional views of neoteny or paedomorphosis and skull base flexion have since been challenged by several German and Swiss anatomists including Beigert, Kummer, Stark and Vogel. Gould (p.378) summarizes their findings as four points: "1. All foetal mammals have a prebasal kyphosis (i.e. a flexed skull base) at the junction of the presphenoid and ethmoid bones. 2. During ontogeny this kyphosis opens out and the face comes to lie in front of the cranium. 3. While the prebasal kyphosis is decreasing in human ontogeny another kyphosis develops within the basi-cranial axis between the basisphenoid and presphenoid bones at the level of the dorsum sellae. This second kyphosis produces a secondary decrease in the spheno-ethmoidal angle following the earlier increase conditioned by the straightening of the prebasal kyphosis. 4. The 'foetal' value of the spheno-ethmoidal angle in human adults does not reflect the retention of a foetal condition (i.e. a strong prebasal kyphosis), but arises from development of the new kyphosis. It is a new feature, not a paedomorphic retention."

Nowadays the "biogenetic law" is usually regarded as a mistaken generalization, but because its effects on the progress of evolutionary biology were, and still are, so profound it is useful to review the ontogenetic changes that occur in the cranial base, so that they can be compared with any proposed sequence of phylogenetic changes derived from observations made on fossil hominids. In this way it is possible to explore the true extent of any parallelisms that exist in the phylogeny and ontogeny of the cranial base, and to be in a position to document the roles of developmental retardation and acceleration during the development of the cranial base.

The literature describing postnatal growth changes in the hominoid cranial base is extremely confusing. Some of this confusion is due to the fact that studies have been carried out for very different reasons. Some studies are concerned with establishing stable points and planes within the cranial base that can be used as reference points for growth studies of other parts of the skull, whereas other investigations are designed to describe growth changes within the cranial base itself. Yet a third group have been concerned with locating sites of flexion within the cranial base.

There is considerable disagreement in the literature as to the precise location of the point of flexion within the cranial base. This is an important problem because this point is usually used to divide the cranial base into anterior and posterior parts and its location obviously influences the angular changes recorded in any study. Thus, this review will begin with a summary of the different flexure points which have been used in growth studies of the cranial base.

The site of cranial base flexion was considered by Huxley (1867), Topinard (1890), Young (1917) and later by Kvinnsland (1971) to be at, or near, the region of the spheno-ethmoidal synchondrosis. However, Cameron (1924), Moss (1958) and Cousin and Fenart (1971) have proposed the region of the pituitary fossa as the axis of flexion, and Björk (1955)

and Sirianni and Van Ness (1978) have suggested the spheno-occipital synchondrosis as the site of flexion.

Recent studies concerned with sites of growth and flexion of the cranial base have employed histological techniques and some have also utilized implant and endosseous staining techniques.

Sirianni and Van Ness (1978), in a longitudinal study using titanium implants in the skull base of Macaca, demonstrated that the inferior part of the spheno-occipital synchondrosis grows at a faster rate than the superior part, thus having the effect of 'rotating' the plane of the synchondrosis so that the basicranial angle is thus gradually opened out during the growth period. Scott (1958) and Michejda (1972) suggest that flexion of the skull base occurs in the region of the midsphenoidal synchondrosis, and halts when the synchondrosis fuses. Scott argues that flexion at the spheno-ethmoidal synchondrosis is unlikely as it would involve a thrusting backwards of the maxilla and palatine bones against the medial pterygoid plates in the facial skeleton. Commenting on Cameron's view that the region of the pituitary fossa is the site of flexion, Scott notes that the midsphenoidal synchondrosis is in fact related to the front of the pituitary fossa, implying that these two flexion sites may be one and the same. Scott does, however, stress that in man, changes could only occur at this synchondrosis before fusion, i.e. before birth, conceding that "changes after birth in man, if indeed they do occur, and if they are not due to measurements incorporating changes in the position of the nasion, are probably due, as Björk (1955) suggests, to changes at the spheno-occipital synchondrosis acting as a site of secondary flexion". Scott considers that this midsphenoidal synchondrosis also closes at birth in the pongids. So it is possible that the increase in the spheno-ethmoidal angle that occurs throughout the growth period in the three great apes (see later) takes place by differential growth at the spheno-occipital synchondrosis in a similar manner to that occurring in Macaca and noted by Sirianni and Van Ness (1978).

Despite the detailed histological descriptions given by several of the above authors, none makes mention of the craniopharyngeal canal. As well as being related to the pituitary fossa in the midline, this canal remains patent in as many as 80% of adult anthropoids (Schultz, 1917; Schlaginhäfen, 1907; Cave, 1930; Randall, 1943, p.313). Schultz (1969, p.164) illustrates the midsagittal section of an infant chimpanzee with a craniopharyngeal canal dividing the body of the sphenoid into two parts. This canal is often said to mark the position of the hypophyseal recess (of Rathke). Arey (1949), however, suggests that this recess is obliterated early in foetal life and that the persistent craniopharyngeal canal represents a vascular channel which is formed later and which passes vertically through the body of the sphenoid bone. Whatever its embryological significance, the canal forms a discrete midline structure in the region of the midsphenoidal synchondrosis and its neglect in the literature on the cranial base is worthy of comment. Michejda (1972) observes that the midsphenoidal synchondrosis was present in juvenile and early adult anthropoid apes that were examined and remarks that when unfused, "it can easily be detected on radiograms in norma lateralis". This important finding is contrary to Scott's earlier belief, and the radiographic appearance of the midsphenoidal synchondrosis and the craniopharyngeal canal clearly needs reinvestigation.

Mention has already been made of remodelling in the region of the pituitary fossa giving rise to a secondary flexion of the human cranial base. Latham (1972) took contact radiographs of 12 soft tissue specimens trephined from the midline region of the human skull at autopsy. This study demonstrated that growth continues at the sphenoidal surface of the spheno-occipital synchondrosis during the first decade of postnatal life in man and that this is coupled with an upward and backward movement of the sella region as the entire pituitary fossa is remodelled posteriorly. Thus, even though Latham reported little indication of an increase in length of the body of the sphenoid bone between the sella and the spheno-occipital synchon-

drosis, growth is continuing here in a superior-posterior direction, so reducing (or maintaining) the degree of flexion of the skull base. This finding also supports Gould's (1977) summary of postnatal skull base flexion in man. It seems most likely from these descriptions that the site of postnatal skull base flexion in man differs from the site, or sites, in the other primates studied as follows. Assuming that Scott is correct and the midsphenoidal synchondrosis closes in man and the pongids at birth, then flexion of the skull base after this time must occur elsewhere. Whereas a secondary posterior remodelling of the sella region would create, or maintain, a flexed skull base in man, a more likely cause in the pongids would be differential growth at the superior and inferior surfaces of the spheno-occipital synchondrosis, similar to that reported for Macaca by Sirianni and Van Ness (1978). Thus, growth studies which interpret the changes during growth of the relative length of the anterior and posterior parts of the cranial base and angular changes in the sagittal axis of the cranial base are best reviewed with these possibilities in mind.

Postnatal growth changes in linear dimensions of the human cranial base

The midline landmarks that are most frequently used in growth studies of the human cranial base are shown in Figure 3. Studies of the anterior part of the cranial base usually use nasion as an anterior reference point, even though this is not at the 'true' anterior end of the skull base. It is worth noting that Huxley (1863, 1867) never mentioned or used the nasion as a marker of the anterior cranial base, defining the plane of the cribriform plate (a line joining the anterior end of the basicranial axis (the prosphenion) and the ethmofrontal suture) as the anterior extension of the basicranial axis. Cameron (1930), however, claims that he did, and arguing that the "strongly curved floor of the olfactory pocket" in lower mammals made it impossible to use this plane as an indicator of the pre-

FIGURE 3.

Midsagittal tracings of Homo sapiens illustrating landmarks and angles used in previous studies of the cranial base:
A Björk (1955), Brodie (1955), Stramrud (1959) and Schulter (1976) B Zuckerman (1955)
C Zuckerman (1955) D Scott (1958) and Fenart and Deblock (1973)
NA nasion, FC foramen caecum, PS prosphenion, PP pituitary point, S sella, BS basion,
OP opisthion, OPN opisthocranion, AL alveolare

pituitary segment of the axis,concluded that "it must be confessed, no other cranial point in the vicinity suggests itself to the writer as a suitable substitute for nasion". It would then appear to be Cameron (1926a, 1927) who first introduced nasion into the literature of the cranial base. In fact, nasion is not a satisfactory point to take as the anterior limit in either linear or angular measurements because it varies in its relationship to the foramen caecum, the point which Scott (1958), probably rightly, considers to be the true end of the anterior cranial base. Scott (1967) also suggests that the position of nasion changes with age, being remodelled upwards as the result of localised growth changes. However, it must be said that Ford (1958) and Björk (1955) found no conclusive evidence for such remodelling in their studies of the human cranial base. Scott (1963) was also at pains to point out that nasion was even less suitable as an indicator of the anterior cranial base in nonhuman primates. However, as Brodie (1955) points out, the fronto-ethmoidal junction in man is almost impossible to determine on radiographs of the skull, so that it has often become necessary to accept nasion as a marker for the anterior end of the cranial base.

The study of Zuckerman (1955) was one of the first to quantify age changes in the human skull base. Zuckerman took lateral radiographs of a large series of human crania with craniometric points marked by lead slugs. Taking nasion and the pituitary point as marking the anterior and posterior extremities of the anterior cranial base; the distance between the pituitary point and basion as the basicranial axis, and the anterior and posterior limits of the foramen magnum as the posterior part of the cranial base, he compared growth changes in these regions by dividing the series of skulls into eight groups based on their developing dentitions. Zuckerman concluded that the anterior part and the basicranial axis continued to grow until after puberty, whereas the posterior part completed its growth by the time the permanent teeth had begun to erupt at about six years. This suggested two growth patterns in the skull base; a neural pattern

completing its growth earlier, and a more general pattern similar to that occurring in the facial skeleton continuing to grow throughout the growth period. Scott (1958) divided the anterior skull base into two parts and recorded growth changes in front of, and behind, the foramen caecum. He concluded that the nasion-foramen caecum distance followed the general growth pattern of the face, whereas the distance between the foramen caecum and the pituitary point followed the neural pattern. This confirmed Brodie's (1941) previous findings. Brodie made lateral head tracings from radiographs of individuals from 3 months to 8 years and showed that the anterior cranial fossa completed its growth early in the growth period. Ford (1958) in a metrical analysis of juvenile human crania, provided considerable support for this view as well as further evidence that the cribriform plate completed growth in both width and length at the very early age of two years. Ford also demonstrated that growth between the pituitary point and the foramen caecum, i.e. presumably at the spheno-ethmoidal articulation, ceased at about the time the first permanent molars completed their eruption. Growth from the pituitary point to basion, however, continued throughout childhood and adolescence. The combined evidence from these studies suggests the following as a reasonably reliable description of growth along the sagittal axis of the human cranial base: (i) The frontal bone between the nasion and the foramen caecum continues to grow throughout the whole growth period: (ii) The cribriform plate ceases to grow at about two years: (iii) Growth at the spheno-ethmoidal suture continues until about six years: (iv) Growth at the spheno-occipital synchondrosis continues during the whole growth period, and: (v) That the foramen magnum attains adult size by six years. Stramrud (1959) has confirmed these suggested human growth patterns in a cross-sectional radiographic study of individuals aged 3 to 25 years, and Björk (1955), in a longitudinal radiographic study of Swedish males from 12 to 20 years, provides evidence for the variation of these changes within a growing population. Knott (1971)

gathered longitudinal growth data and found a similar pattern of changes in the growing human cranial base. Latham's (1962) study has already been mentioned with reference to its discussion of secondary remodelling in the region of the pituitary fossa. In it he also showed that the distance from the sella to the spheno-occipital synchondrosis, and from the posterior wall of the pituitary fossa to the same synchondrosis, did not increase in humans after two years of age. This suggests that the body of the sphenoid as a whole does not increase in length in the posterior direction after two years, and if the data of Ford and Brodie, which indicate that growth of the anterior cranial fossa ceases at six years, are taken into consideration, then it follows that any increase in the length of the body of the sphenoid after two years must be occurring at the spheno-ethmoidal articulation. Even here, however, growth ceases at the age of six or seven. Hoyte (1975), in a review of growth in length of the cranial base, supports this conclusion. Ford (1958) also provides data indicating that the ethmoidal air cells continue to grow in width across the interorbital region until adulthood, in much the same way that the frontal air cells continue to do.

Postnatal angular changes in the sagittal axis of the human cranial base

Postnatal angular growth changes in the human skull base have been investigated by most of the authors mentioned in the preceding sections and a variety of landmarks have been taken to be the site of Flexion. The angles that have been studied most often are the spheno-ethmoidal and foramino-basal angles, and the midline landmarks that have been used to form them are illustrated in Figure 3.

Virchow (1857) was probably the first to observe a general decrease in the cranial base or "saddle angle" from birth to puberty in modern Homo sapiens. However, Zuckerman (1955) was the first to measure age changes occurring at the spheno-ethmoidal angle in a series of 190 European

skulls ranging in age from one year to aged individuals. Using either prosphenion or the pituitary point as the point of flexion, he found that in both cases this angle decreased with age; for prosphenion the reduction was from 152° to 149° and for the pituitary point from 143° to 132°. These angular changes are much less pronounced than the changes which occur in the linear dimensions of the cranial base. Björk (1955), using tracings of lateral head radiographs of Swedish boys taken at 12 years and again at 20 years, provided evidence for angular growth changes occurring later in the growth period. Björk showed that the angle nasion-sella-basion increased in some instances and decreased in others by a maximum of 5° either way, but about a mean of 131° (at both 12 and 20 years). When the radiographs were superimposed on the nasion-sella line, Björk demonstrated that an increase in the degree of flexion of the basicranial axis (sella-basion in this study) were associated with a lowering of the foramen magnum and a downwards and forwards displacement of the temporal bones, and hence the glenoid fossa. When the angle increased, the opposite sequence of events occurred. Brodie (1955), in a longitudinal study utilizing lateral skull radiographs, measured the basicranial angle, taking sella as the point of flexion, and observed a considerable variation in the way the angle behaved during growth. The nasion-sella-basion angle increased in some individuals and decreased in others by about 5° either side of a mean of 131°, with a range of 120° - 143° in the adults. Out of a total of thirty cases, twelve showed no change at all from four years to 18 years, while of the eighteen cases which did show any angular change, in only five was there change of more than 4°. Stramrud (1959), in a radiographic study, compared the nasion-sella-basion angle with the foramen caecum-sella-basion angle and concluded that both angles, on average, remained unchanged from 3 years to adulthood. The difference between the two angles ranged from 3° - 4° in the early ages, to 4° - 5° nearer to adulthood, this difference presumably being due to nasion rising slightly.

The correlation between the two angles for the total sample was high ($r = 0.86$).

A defect of all these studies is that they provide little good data for very early changes in the nasion-sella-basion angle before three years of age. George (1978) has made a particular study of angular changes at this early stage and, using several landmarks to trace skull base flexion in a longitudinal radiographic study, she concludes that all angles measured showed a decrease from birth to three years. The reduction ranges from 7^{o} to 14^{o} depending on the landmarks chosen. The change in the nasion-sella-basion angle was about 11^{o}, i.e. from 143^{o} at one month after birth to 132^{o} at three years.

Zuckerman (1955) also measured the foraminobasal angle (this angle was first described by Huxley (1863)) which indicates the slope of the foramen magnum relative to the basicranial axis. When the pituitary point was used as the anterior terminus for this angle, it measured 130^{o} at birth and increased during the period the foramen magnum was growing to 141^{o} and then decreased again to a mean adult value of 132^{o}. However, when prosphenion was used as the anterior terminus, there was no change in this angle during the growth period. Moss (1958) cites the occipital region of the skull in man as having the greatest postnatal neurocranial growth rate. This is reflected in the relative growth rates of both the occipital bone and the cerebellum which expand laterally and rotate downwards relative to the face. Fenart (1953) has also drawn attention to this and has measured the angle the foramen magnum makes to the horizontal semicircular canal during growth of the skull. He records an increase of some 28^{o} throughout the total growth period.

Postnatal changes in the human cranial base other than in the sagittal axis

Some studies have extended investigations in the sagittal plane to include measurements of width across the midline. Nakamura, Savara and Thomas (1972) provide good longitudinal radiographic data for incremental growth of the sphenoid bone between the ages of 4 and 16, and Knott (1974) gives additional information for biforamen rotundum growth from 6 years to adulthood. These data for the growth patterns of an individual bone are especially useful when interpreting the pattern of growth in the cranial base as a whole. Two patterns of growth are clear. The growth pattern of the dorsal surface of the sphenoid bone, which forms the floor of the cranium, resembles the growth pattern of the brain and neurocranium, with most of the growth occurring before 10 years of age and with little, or no, discernable adolescent growth spurt. In contrast, the ventral surface of the sphenoid lies at the posterior boundary of the facial skeleton and, like the facial bones, has a distinct adolescent growth phase, as well as growing at a greater rate overall than that of the dorsal surface. Nakamura et al (1972) demonstrated that between the ages of 4 and 16 years there is an increase of only 5 mm in the length of the body of the sphenoid bone in both sexes. Most of this occurs in the posterior part of the sphenoid and very little in the presphenoid. These results thus generally lend support to the findings of the earlier cross-sectional studies of Brodie (1941), Ford (1955) and Scott (1958).

Comparative growth studies of the cranial base in primates

The studies of Bolk (1909, 1910), Keith (1910), Duckworth (1915) and Cameron (1926) examined the growth of the cranial base in comparative primate material but the study of Ashton (1957) provided the first reliable comparative data for growth of the cranial base in primates. Ashton provides extensive cross-sectional data for large samples of Pan, Gorilla,

Pongo, Papia and Macaca. Ashton used the radiographic technique developed by Zuckerman (1955), and also grouped skulls into dental developmental subsets. He used the pituitary point, and not the prosphenion, as the point of flexion of the skull base following Zuckerman's findings in man that age changes in the foraminobasal angle could only be revealed when the pituitary point was used as the anterior point of the basicranial axis. Ashton also avoided using the nasion, because of "the peculiar formation of the nasal bones in the anthropoidea". Instead, he defined the anterior limit of the cranial base as "the point where the line joining the upper limits of the frontal processes of the maxillae crossed the sagittal plane". Scott (1958), however, remarks that "even this point lies well above the level of the foramen caecum in these animals because the cribriform plate and the foramen caecum lie at the bottom of a deep olfactory pocket, but despite that, the foramen caecum probably represents more accurately than any other the true anterior end of the cranial base". Scott (1963) has demonstrated that in the non-human primates, values for the spheno-ethmoidal angle are about 10^{o} higher when the nasion is used to form the cranial base angle in preference to the foramen caecum. Ashton found that in all primates studied, the spheno-ethmoidal angle continues to increase until maturity and that the foraminobasal angle in primates gradually decreases during the growth period. Ashton gives the mean adult values for the spheno-ethmoidal angle as 157^{o} for Pan, 165^{o} for Pongo and 168^{o} for Gorilla (increasing by 8^{o}, 7^{o} and 9^{o} respectively during the postnatal growth period in each taxa). Mean adult values for the foraminobasal angle are given as 121^{o} for Pan, 116^{o} for Pongo and 123^{o} for Gorilla (falling by 5^{o} in Pan and Gorilla and by 7^{o} in Pongo during the postnatal growth period). Ashton remarks that "bursts of growth" in the basicranium occur in Gorilla and Pongo when the canines and third molars are erupting, especially in the distance from endobasion to the pituitary point,

dentition due to the development of the nuchal and sagittal crests. Schultz (1955) projected the position of the condylion onto the nasion-basion line of many different primate skulls of differing ages, and also noted the relatively forward position of the condyles in the young of all types of primates and their posterior displacement during the growth period. The exception to this is in man where the juvenile condition is retained throughout life. Ashton and Zuckerman (1956, a) have also described growth changes in the position of the foramen magnum in Gorilla, Pan and Homo sapiens. By relating the position of endobasion to the positions of prosthion, glabella, and opisthocranion projected parallel to the Frankfurt Horizontal, indices were calculated which demonstrate that the foramen magnum follows a similar growth pattern to that previously demonstrated for the occipital condyles by Ashton and Zuckerman (1952).

Since the preliminary investigations of Ashton et al, several authors have confirmed these general findings in anthropoids. Fenart and Deblock (1973) have provided data for some 148 linear and angular measurements for a series of 179 specimens of Pan troglodytes and 83 specimens of Pan paniscus. All the specimens were divided into seven groups, each corresponding to a dental developmental stage, and growth in each of the variables was compared. Their results provide evidence of an increase in the cranial base angle (i.e. foramen caecum-sella-basion) from 138^{o} to 146^{o} during the postnatal growth period for Pan paniscus, and an increase from 149^{o} to 152^{o} during the same period for Pan troglodytes. While it must be admitted that the group sizes are small, it is interesting to note that the mean values of foramen caecum-sella-basion angle for the juvenile groups of Pan troglodytes and Pan paniscus differ by 10^{o}. Fenart and Deblock also provide data for growth in width of some bilateral structures of the cranial base. Their results suggest a rapid rate of growth in biporionic and bimastoid widths, when compared with the much slower growth in width

and in the anterior part of the cranial base to nasion. No adolescent spurts were noticed in the other species, but there was a considerable increase in these dimensions in all the species examined during the period when the permanent incisors, second molars and premolars were erupting. The posterior part of the cranial base (i.e. the length of the foramen magnum in the sagittal plane, in this study) attained adult size in all species by the time the first permanent molars were in occlusion. Ashton and Spence (1958), in a later paper, confirmed that the foramen magnum attains 95% of adult size by the time the first molars are in occlusion, and thus follows a similar pattern of endocranial growth in both man and pongids.

These results from pongids contrast with those of the human studies in several ways. No clear evidence of an adolescent spurt has been documented in human longitudinal studies, although Zuckerman (1955 in his early cross-sectional study, says that the basioccipital, basisphenoid, presphenoid and ethmoid bones all take part in a "burst of growth" in an anteroposterior direction during adolescence in man. In contrast with other primates, the foraminobasal angle in man does not begin to decrease until after the beginning of the eruption of the permanent teeth. Between birth and this time, the angle increases, continuing a trend established during foetal life. The human spheno-ethmoidal angle decreases after birth in the period up to the eruption of the deciduous teeth and thereafter remains fairly constant. Thus, these particular angular changes would appear to be special human characteristics.

Growth changes in the position of the foramen magnum and occipital condyles in the higher primates were investigated at an early stage by several authors, notably Bolk (1909, 1910). Ashton and Zuckerman (1952) reported age changes in the position of the occipital condyles in Pan and Gorilla and concluded that there is a steady fall in the condylar index (i.e. a relative posterior displacement of the condyles) in both taxa. The values for Gorilla do, however, rise slightly after eruption of the permanent

of the foramen magnum; the growth in length of the foramen magnum stops earlier. Cramer (1977) also provides data for the foramen caecum-pituitary point-basion cranial base angle in both species of Pan. He quotes the mean angle in humans as 135° and his own values for Pan paniscus and Pan troglodytes of 140° and 145° respectively. Ashton (1957), using his definition of nasion, gives the mean value of the spheno-ethmoidal angle of Pan troglodytes as 159° for males and 156° for females. This is on average up to 14° higher than that quoted by Cramer using the foramen caecum to measure the same angle, but only 7° more than that (152°) given by Fenart and Deblock (1973). Lestrel and Moore (1978) have suggested that the cranial base angle is unsuitable for any detailed analysis of the changes observed in the cranial base during growth. They see the major difficulties as the complex morphology of the cranial base and the inability to distinguish clearly between the effects of size and shape. Applying Fourier analysis to midsagittal radiographs of the cranial base, Lestrel and Moore have developed a method of accurately measuring the irregular form of the endocranial profile of Macaca nemestrina while minimizing the effects of size and enhancing shape differences. Laitman (1977) and Laitman, Heimbuch and Crelin (1978) have recently extended these comparative growth studies by recording the degree of exocranial base flexion on a large sample of primate crania. Through the use of multivariate and discriminate analysis, coordinate values were derived from nine linear measurements taken between five craniometric points on the skull. A line representing the shape of the cranial base on its exocranial surface was constructed. The axis was defined as being parallel to the horizontal line of the palate from prosthion to staphylion and the Y axis at right angles to it. By using successive approximations to best fit the position, X and Y coordinates for hormion, sphenobasion and basion were determined.

Using the plane of the palate as reference plane is unusual. Beigert (1957, 1963) demonstrated how much variation there is in masticatory

adaptations within primates, and how characteristics of the skull base are influenced by craniofacial changes and interspecific differences in the masticatory apparatus. These in turn are largely dependent upon body size, a factor which Laitman et al (1978) regard as "being of interest, but too complicated to discuss and not a major concern" in their study. There is, however, evidence in Homo that the nasion-sella line remains almost parallel to the horizontal line of the palate, moving only directly downwards during growth of the face (Brodie, 1955; Björk and Skeiler, 1972) but evidence to the contrary has been adduced for the three great apes (Krogman, 1931, a,b,c). Laitman et al follow other workers and divide their juvenile sample into several subsets based on dental development in order to study changes in exocranial base flexion during growth in each taxa. The relationship of exocranial base flexion to the more usually studied endocranial base flexion is not made clear in this study, and thus comparison with previous studies of the skull base is very difficult. However, the studies by Laitman and his co-workers do demonstrate important ontogenetic differences between humans and nonhuman primates. Newborn humans exhibit little exocranial base flexion between the hard palate and the foramen magnum. During growth, the human cranial base develops in a unique way which results in marked flexion between the posterior margin of the hard palate and the foramen magnum. It would appear from the diagrams of these changes (Laitman, 1977), that after the eruption of the deciduous dentition, i.e. about two years of age, little change in the orientation of the external surface of the basioccipital occurs, suggesting that early 'flexion' in this region closely parallels the decrease in endocranial flexion which has been shown to be taking place at the same time (George, 1978). The exocranial flexion is further exaggerated during growth by a backward and upward movement of the vomer as the face comes to lie deeper under the neurocranium. In contrast to this pattern of human development, the exocranial cranial base of the pongids (and other

primates) while similar to man at birth, shows a decrease during development in the angle between the hard palate and the foramen magnum. The spheno-occipital synchondrosis, foramen magnum and basiocciput become gradually elevated relative to the palate throughout growth. It seems likely that this accompanies the increase in endocranial skull base flexion that occurs in the pongids, the foramen caecum-pituitary point-basion angle increasing with age. It may also be related to the fact that the face (and palate) come to lie increasingly anterior to the neurocranium, a feature described and illustrated long ago for all three great apes by Krogman (1931, a, b, c). Laitman et al (1978) suggest that "the effect upon the basiocciput produced by the descent of the tongue and larynx in man may well be one of the factors which relate to the shape change in the incline of t he basioccipital, and the establishment of exocranial base flexion via the insertion of the pharyngeal constrictor muscles and the midline raphé onto the pharyngeal tubercle". Sonntag (1924), as will be discussed later, also noted the more horizontal arrangement of the constrictor muscles in the pongids in contrast to those of modern humans, but interestingly, attributed this to prognathism of the jaws in the pongids. Laitman (1977) and Laitman et al (1978) do not discuss the possibility that differences in size and shape of the jaws (for example, height of the mandibular ramus and the degree of mandibular prognathism) may contribute to differences in the comparative anatomy of the larynx and nasopharynx. They appear to assume that there is a simplistic relationship between the cranial base and the upper respiratory structures which is unaffected by other adaptive modifications that occur in the neurocranium and in the masticatory system of primates.

It is generally accepted that juvenile primates resemble one another more closely than adults. Clearly differences in the growth patterns of the cranial base largely underlie the differences that are observed in adult hominoids. As Baer (1954) notes, differences in form and proportion

among fossil and living groups are due to changes in relative rates of growth. That being said, however, the growth processes in the cranial base and face which result in flexion and extension in the skull as a whole, are still not fully understood.

CHAPTER 3.

The soft tissues associated with the hominoid basicranium

Introduction

The soft tissue anatomy of modern man, and the relationship of the soft tissues to bony landmarks on the skull base, such as crests, tubercles, processes or fossae, are well documented in standard textbooks of human anatomy. However, bony landmarks on the skull base of other primates cannot be automatically associated with homologous soft tissue structures, as these do not always take the same form as those of modern man. The myology of the head and neck of the extant hominoids, and the processes that determine the corresponding bony surface markings are both complicated subjects. It is , however, foolhardy to attempt to establish homologous landmarks between man and the extant pongids with any degree of reliability, or to go on to interpret features of the cranial base of fossil hominids, without a detailed appreciation of the comparative background and the interaction between bone and soft tissue structures. Thus, before reviewing the comparative myology of the skull base region in pongids, I shall briefly review studies which have been concerned with the general behaviour of bone at the muscle-bone interface, and with the factors involved in the formation of bony surface markings.

The bone-muscle interface

It is widely accepted that the detailed shape of any bone results in part from patterns of muscle forces acting upon it. Muscle pull is regarded as the primary force responsible for the formation of elevated tubercles, tuberosities and crests upon which they are attached (Washburn, 1947; Scott, 1957). Tension exerted by these muscles is presumed to stimulate local osteogenesis and to increase the mass of bone beneath the muscle,

thereby producing an elevated area of insertion. However, the actual mechanism by which tension or pressure can be translated into either osteoblastic or osteoclastic activity is not known. The generally accepted view of the nature of the external form and of the internal structure of bone is known as Wolff's Law (Wolff, 1892). This is usually expressed in the following way: 'Every change in the form and function of a bone, or of the function alone, is followed by certain definite changes in the internal architecture and definite secondary alterations in the external conformation in accordance with mathematical laws." Two views concerned with the effects of functioning muscles on skeletal tissues have grown from the original work of Wolff. The results of more recent studies by Moss et al (e.g. 1960, 1969, 1978) have become known, and summarized, as the 'Functional Matrix Hypothesis'. This hypothesis considers that "the presence, form (i.e. the shape and size), growth and position in space of skeletal tissues (called the skeletal units or Sk.U) are secondary, compensatory and mechanically obligatory responses to the temporally (and morphologically) prior demands of related functional matrices (FM)" (Moss, 1969). For example, Moss (1970) has demonstrated that decreases in size and alteration in shape of the coronoid process are directly related to the amount and position of functioning temporalis muscle fibres remaining after experimental partial myectomy.

There is however, another view that while not dismissing these ideas completely, maintains that simple muscle pull is inadequate in itself to account for the varied and complex processes of remodelling that accompany the growth of a bone. Many of the original criticisms of Wolff's Law (e.g. see Murray, 1936) were made by those who adhered to a 'primary' or 'inherent' growth pattern theory as the causative factor in the production of bone form and architecture. Wolff, however, made no reference to the process of growth or to the means by which the final structure is formed, referring only to the final functioning structure of a bone. There is,

however, evidence to suggest that the law may hold good for some of the changes that occur during growth (Townsley, 1948). Many bony crests or fossae appear towards the end of the growth period in cranial bones and it is interesting to note that Fisher et al (1976) have demonstrated that forces or 'unit strains' in skulls are greatest during infancy and childhood, even though it is during early adulthood that the majority of bony surface details become most marked. Experiments removing important growth centres in the cranial bones of animals (DuBrul and Laskin, 1961) demonstrate that shape and form are at least as equally dependent upon an inherent growth pattern as they are upon functioning muscles, or the influence of the growing brain (Moss, 1975). A further argument against muscles being the only causative factor in bone remodelling arises from suggestions that experimental myectomy necessarily involves the destruction of the periosteal blood supply, and so would be expected to promote resorption of the underlying bone (Boyd, Castelli and Huelke, 1967). These authors further argue that removing the functioning muscle from its origin, but leaving the insertion intact, does not appear to have the same effect as myectomy on the insertion. This suggests that vascular changes might be as important as muscle tension.

Hoyte and Enlow (1966) have also argued that bony tubercles, crests and other elevations are being continuously moved and relocated in order to maintain constant relative positions on the enlarging bone as a whole (see also Keith, 1910). As a result of these complex remodelling changes, a great many areas of the outer surface of a bone are actually resorptive, including the surfaces of many tuberosities and elevations. Further, a single muscle is often attached onto a bony surface, part of which is undergoing deposition while the rest is simultaneously undergoing resorption. Hoyte and Enlow conclude "to state that muscle tension or pull is directly related to the building up of a bony elevation to the exclusion of all other remodelling changes is not warranted". They do, however,

concede that these observations do not contradict the principle that muscle action can influence the morphology of bone, merely that the mechanism of this change is more complicated than is generally appreciated. Dörfl (1980 a, b) has demonstrated that the cause of muscle attachment migration is the growth of periosteum "dragging the attachment during its stretching" which is itself caused by growth of the bone. Dörfl has also demonstrated that muscular traction does not seem to play a decisive role in migration, which is limited to the period of growth of the bone and periosteum and ceases with the end of this period, although the muscles may enlarge after this time.

There are several other potentially important factors that may affect the development and structure of bone at the muscle-bone interface and thus influence the interpretation of such features as crests, tubercles and fossae on the skull base. Early foetal muscle fibres, formed after motor nerve innervation, are preferentially orientated towards the site of their future attachments although these attachments to bone occur later in development (Rayne and Crawford, 1971). This foetal orientation of muscle fibres suggests a predetermined pattern for muscle attachment which only becomes manifest later in development (Sperber, 1976).

Muscles attach either to periosteum or to bone as broad aponeurotic sheets, or as circumscribed tendons or ligaments. Periosteally attached muscles end by their terminal epimysial fibres blending with the fibrous periosteum covering the smooth, or slightly roughened, surface of the bone (Moss and Moss-Salentijn, 1978). Generally, aponeuroses end in extensive, thin, bony crests, while tendons are associated with convex spines or tubercles, or with concave grooves or pits (Dullemeijer, 1974). At aponeurotic attachments the majority of the fibres of the aponeurosis end in the fibrous periosteum, but a few larger fibres continue into bone as uncalcified Sharpey fibres. Tendonous attachment sites are more complex.

Unlike aponeurotic attachments, where the bone remains 'laminar', tendonous sites form an inwardly radiating trabecular attachment area. The bony trabeculae and the incoming fibres share a common orientation. Tendon fibres do not pass directly into bone but end in a thickened periosteal mass. A second 'relay' of collagen fibres run from the periosteum directly into the bone mass and are usually calcified (Moss and Moss-Salentijn, 1978). Many muscles combine a smooth periosteal attachment with a tendonous or aponeurotic attachment which is associated with a roughened area or raised crest at the margin of the muscle attachment. Scott (1967) has suggested that "where growth of the skeleton is in excess of the requirement of muscle tissue the 'unwanted' muscle becomes converted into tendon, this being a common phenomenon in the limbs". It also means that where there is a tendonous insertion, movement or contraction of muscle fibres does not occur near the bone-muscle interface. This may be an important influence in the formation of surface elevations. Moss and Moss-Salentijn (1978) suggest that there are richer vascular interconnections between bone and muscle at the sites of fleshy (periosteal) attachments than at the sites of tendonous attachments, and imply that surface markings may well be influenced by different degrees of vascularity at the bone-muscle interface. They suggest that the alterations in periosteal vascularity may be a response to changes occurring at the bone surface and not the cause; regions of rich vascularity being associated with areas of resorption and areas of reduced vascularity being associated with areas of deposition.

Bassett (1971) has proposed that bone remodelling may be mediated by differences in electric potential. This theory stems from the discovery that bone is piesoelectric, that is, when it is mechanically deformed it generates an electric potential. Bassett established that the electric potential generated was proportional to the force applied and that on bending pieces of bone, the convex side under tension was positively

charged and the concave side under compression was negatively charged. Bassett showed by experiment that negatively charged surfaces of bone were found to induce new bone formation even though no resorption occurred on the positively charged surfaces. Osteogenesis in response to compression is the reverse of the usually accepted view that osteogenesis occurs in in response to tension. It seems likely that the electrical effects demonstrated by Bassett are important in understanding bone remodelling, but the situation is undoubtedly more complicated than has so far been appreciated. Moss (1978) has pointed out that the 'streaming potential' produced by the flow of blood through blood vessels in bone may be related to the way in which it responds to vascularity at the bone-muscle interface.

It is clear that the concept of muscle tension being the primary force directly responsible for the formation of surface details on bone is too simplistic to account for all the changes at the bone-muscle interface. Scott (1967) is probably near to the truth when he states that "during the time of growth, heredity and function overlap in their task as bone-producing and bone-forming elements". It is more than likely that many of the processes, tubercles and fossae characteristic of either the modern human or pongid skull base are as closely related to embryological and developmental features as they are to the local effects of muscle tension.

Comparative myology of the cranial base and nuchal regions in hominoids

Introduction

Anecdotal accounts of the two African apes go back to 500 B.C. when Hanno set out to explore the West Coast of Africa and returned with accounts of "wild men" and the skins of specimens they had killed. Edward Tyson (1650-1708), an English anatomist, was the first to dissect and describe a young chimpanzee in 1699. His book, published by the Royal Society, entitled "Orang-outang Sive Homo Sylvestris: or the anatomy of a pygmie

compared with that of a Monkey an Ape and a Man", is the first account of an ape which "has any pretensions to scientific accuracy and completeness" (Huxley, 1863). Peter Camper (1722-1789), a Dutch anatomist, published a similar treatise on the orang utan (Camper, 1779, 1803). Camper dissected several females and one male and was the first to give a clear account of the distinctiveness of the "true East Indian Orang".

The first authoritative and trustworthy reports of the gorilla were published in 1847. Thomas Savage and Leighton Wilson, two early missionaries to West Africa, despatched descriptions and specimens of skulls to two comparative anatomists, Richard Owen in London and Jeffries Wyman in Boston, U.S.A. Owen, who had already dissected an orang utan in 1831 and described the osteology of the chimpanzee and orang utan in 1835, regarded the two gorilla specimens as a large species of chimpanzee Troglodytes savegei (Owen, 1848, 1851). Savage and Wyman had already published descriptions of the specimens (1847, a and b) giving them the scientific name Troglodytes gorilla. It was not until 1851 that the French naturalist Isidore Geoffrey Saint-Hillaire proposed a separate genus for the new ape, on the basis of such distinctions as the massive cranial crests, the shape of the teeth and the disparity in size between the sexes. It was, however, not until 1873 that Macalister published the first account of the muscular anatomy of the gorilla.

This review of the literature of the comparative myology in the region of the skull base of Homo sapiens, Gorilla gorilla, Pan troglodytes and Pongo pygmaeus is presented in two sections. The first section presents a broad review of the differences between the myology of the head and neck of modern humans and pongids, and the second sets out details of the prevertebral, upper pharyngeal, deep and superficial mastoid, and nuchal muscles in Homo sapiens and the pongids.

Comparison of the head and neck myology of Homo sapiens, Pan troglodytes, Gorilla gorilla and Pongo pygmaeus

The neck of Gorilla, Pan and Pongo is massive, and contrasts with the relatively thinner and longer neck in humans (see Schultz, 1969). The secondary cervical curvature and shortened cervical spinous processes also contribute to the smaller size of the human neck. Tyson (1699) was the first to document anatomical details of Pan, and among these was a reference to a large muscle of the neck, the levator claviculae. This muscle, as Parsons (1898) remarks, "is a very constant muscle in mammals, but only occurs in man as an abnormality". It is present in all three great apes and takes origin from the transverse process of the atlas and is inserted into the lateral end of the clavicle. Sonntag (1923), however, describes the site of insertion in a young female chimpanzee as to the "upper outer end of the acromion". Parsons (1898) regards this acromional insertion as the usual mammalian condition, specifically stating that "the anthropoid apes and the bats were the only two exceptions". This muscle, together with the massive trapezius, accounts for much of the width of the base of the pongid neck. All these authors mention that the levator claviculae can have an occipital origin as well as, or instead of, its origin from the atlas. These confusing variations of origin and insertion probably underlie the equally confusing number of names that this muscle has been given in the anatomical literature - Omo trachelian (tracheleo - Gk. neck); atlanto clavicularis; atlanto cervicalis; atlanto scapularis; omo atlantic; and trachelo acrominal are some of the names that have appeared in the literature. However, as its usual origin in the three great apes appears to be the transverse process of the atlas, and as the majority of authors including Wyman (1855), Humphry (1867), Macalister (1871, 1873), Raven (1950), Miller (1952), Swindler and Wood (1973) consistently describe a clavicular insertion, it will be referred to as atlanto clavicularis in this

review. Parsons (1898) suggests that this muscle is an "extension of the same sheet of muscle as the trapezius in man that has had to seek a deeper origin, but still always being supplied by the second, third and fourth cervical nerves". Owen (1831) regards the atlanto clavicularis as a variation of the levator scapulae and not the trapezius. In an account of a human dissection where an atlanto clavicularis was present, Flower and Murie (1867) make clear that the muscle was firmly adherent to the underlying splenius and was lying lateral to the trapezius; this observation would therefore seem to favour Parson's explanation. The great breadth of the pongid neck may in part account for the extensive air sacs that communicate with the larynx in all three great apes, it being rather more economic to 'fill in' the spaces between widely separated neck muscles with air sacs than with much denser fibrous connective tissue. Other theories put forward to explain their presence include the suggestion that they function as resonators, supporters of the jaws, or part of an adaptation to a herbivorous diet (Hilloowala, 1969).

The general arrangement of the nuchal muscles in the three great apes is significantly different from that in man. Where there are crests, either nuchal or sagittal, the soft tissues rise off the crests proud of their origin, and it is clear that the temporalis usually has no part in the formation of the nuchal crest for it normally does not extend down to it, and in pongids occipitalis muscle takes origin from the superior lip of the nuchal crest. This can clearly be seen in the dissection illustrations of Bluntschli (1929), Raven (1950) and Swindler and Wood (1973). The platysma myoides, a remnant of the cutaneous panniculus carnosus muscle that completely envelops the greater part of the body in lower mammals, can extend dorsally right to the midline in the apes to envelop the nuchal muscles; however, it is not so extensive in Pan and Gorilla as it is in Pongo (Parsons, 1898; Sonntag, 1924; Lightoller, 1928). No ligamentum nuchae exists

in the apes, a factor associated with the lack of any marked bony external occipital protuberance (Sonntag, 1924; Owen, 1831). The trapezius in Pan arises from the inner third of the occipital crest, and from a much more extensive area in Gorilla and Pongo.

In man the rhomboid muscle is usually differentiated into major and minor parts. This is not so in the pongids and it is usual to find an occipital origin for this muscle in Pongo. Owen (1831) attributes this "broad adherence of the rhomboidei to the occipital bone beneath the trapezius" to the need for additional support for the head. An occipital origin for the rhomboideus in Pan has been described by Gratiolet (1866) but this is unusual, and other descriptions of chimpanzee myology, e.g. Champneys (1872), make no mention of this. Macalister (1873), Chapman (1878) and Raven (1950) suggest that an occipital origin in the gorilla is not the normal situation, although Sonntag (1924) states that the origin of rhomboideus extends from the spine of the axis to a point which varies from the third to the sixth dorsal vertebral spine.

The literature dealing with the pongids contains few detailed descriptions of the semispinalis (or complexus) or sternocleidomastoid muscles, or of the muscles of the suboccipital triangle and their attachments. Nonetheless, several general points are worthy of mention. The semispinalis is a complicated muscle which varies among the three apes. Sonntag (1924) states that two parts are recognisable in Gorilla and Homo ; a more medial 'biventer' (so named because of a tendon which intervenes between two fleshy bellies-Gray's Anatomy, 15th edn.); and a lateral 'complexus' part. Raven (1950) also mentions a spinalis capitis and a semispinalis in his dissection account. Three chimpanzees dissected by Sonntag (1924) showed no trace of this division, which Swindler and Wood (1973) later suggested is the usual condition. No details are available for the orang utan.

Muscles in the larger bodied pongids often appear to have several heads, where there is usually only one in man. For example, the sternocleido-

mastoid is in the form of two quite distinct muscle bellies until its insertion into the mastoid area in all pongids (Sonntag, 1924), and the superior oblique and rectus capitis posterior major are often described as arising as two, or more, heads in the larger apes. This, however, is not true of the splenius which in all three apes is a powerful muscle with an extensive insertion which runs from the mastoid to the midline along the nuchal crest (Sonntag, 1924).

General differences in the myology of the head and neck of the apes and man also occur in the accessory muscles of mastication. The anterior bellies of the digastric are often fused in Pan and Duckworth (1915) points out that the size of the anterior bellies is inversely proportional to the size of the mandible. Hence it might be argued that, with a lighter mandible, man requires a stronger depressor, and with a widened space between the mandibular tooth rows, also requires more sublingual support for the tongue. The orang utan is unique in that the anterior belly has been lost altogether, the posterior belly inserting into the angle of the mandible below the insertion of the medial pterygoid. The anatomy of the floor of the mouth is thus quite different, with the fibres of the mylohyoid also reduced, decussating in the midline without an intervening raphé. Parsons (1898) considers that the anterior belly is the phylogenetically older part of the digastric muscle, the posterior belly being derived or 'split off' from the stylohyoid later in time. Parsons goes on to suggest that this may be the reason why absence of the anterior belly of the digastric is rare in man but absence of the stylohyoid fairly common. Clearly, whatever the phylogeny of the muscle, the function of the digastric as a depressor of the mandible in the orang utan is biomechanically quite different to that in man and the other two great apes.

Unlike the condition in man, in all three great apes, the platysma has an extensive insertion on the lower border of the mandible (Lightoller, 1928; Blutschli, 1929; Raven, 1950) and may also be involved in depression of the mandible.

Details of the muscles of the pharynx, palate and mastoid regions in higher primates

This section reviews the detailed myology of the prevertebral and pharyngeal musclature, first in Homo sapiens and then in the comparative pongid taxa. The comparative myology of the mastoid and nuchal regions in both Homo sapiens and Pan, Gorilla and Pongo are then reviewed together.

Most textbooks of human anatomy describe the superior constrictor muscle as taking origin from the pharyngeal tubercle on the basioccipital. This has been challenged by Takagi, Walters and Bosman (1962), who claim that the muscular pharyngeal wall extends dorsally only as far as the spheno-occipital synchondrosis, the pharyngeal tubercle itself marking the attachment of the investing fascia. The levator palati muscle in man takes origin by a cylindrical tendon from a roughened area on the underside of the petrous apex adjacent to the carotid foramen, and also from the tubal cartilage (Klueber and Langdon, 1979). It descends anteromedially, along the course of the eustachian tube, crossing the superior constrictor, to fan out into the superior aspect of the palate. Rowan and Turner (1956), in a dissection study of sixteen adult and four foetal human specimens, noted an additional head for levator palati arising from the carotid sheath. The tensor palati takes origin from the spine of the sphenoid, the tubal cartilage and the scaphoid fossa of the medial pterygoid plate. The fibres descend inferolaterally, in a fan-like manner, to converge at the pterygoid hammulus as a tendon which rounds the hammulus to insert into the margin of the palatine bone and blend with the palatine aponeurosis. It is a triangular shaped muscle situated lateral to the superior constrictor, lying between it and the cranial base. Lateral to the tensor palati lies the medial pterygoid muscle and inferomedially the levator palati. Posterior to the pharyngeal wall, two more pairs of muscles attach to this region of the cranial base, the rectus capitis anterior and the longus capitis (or

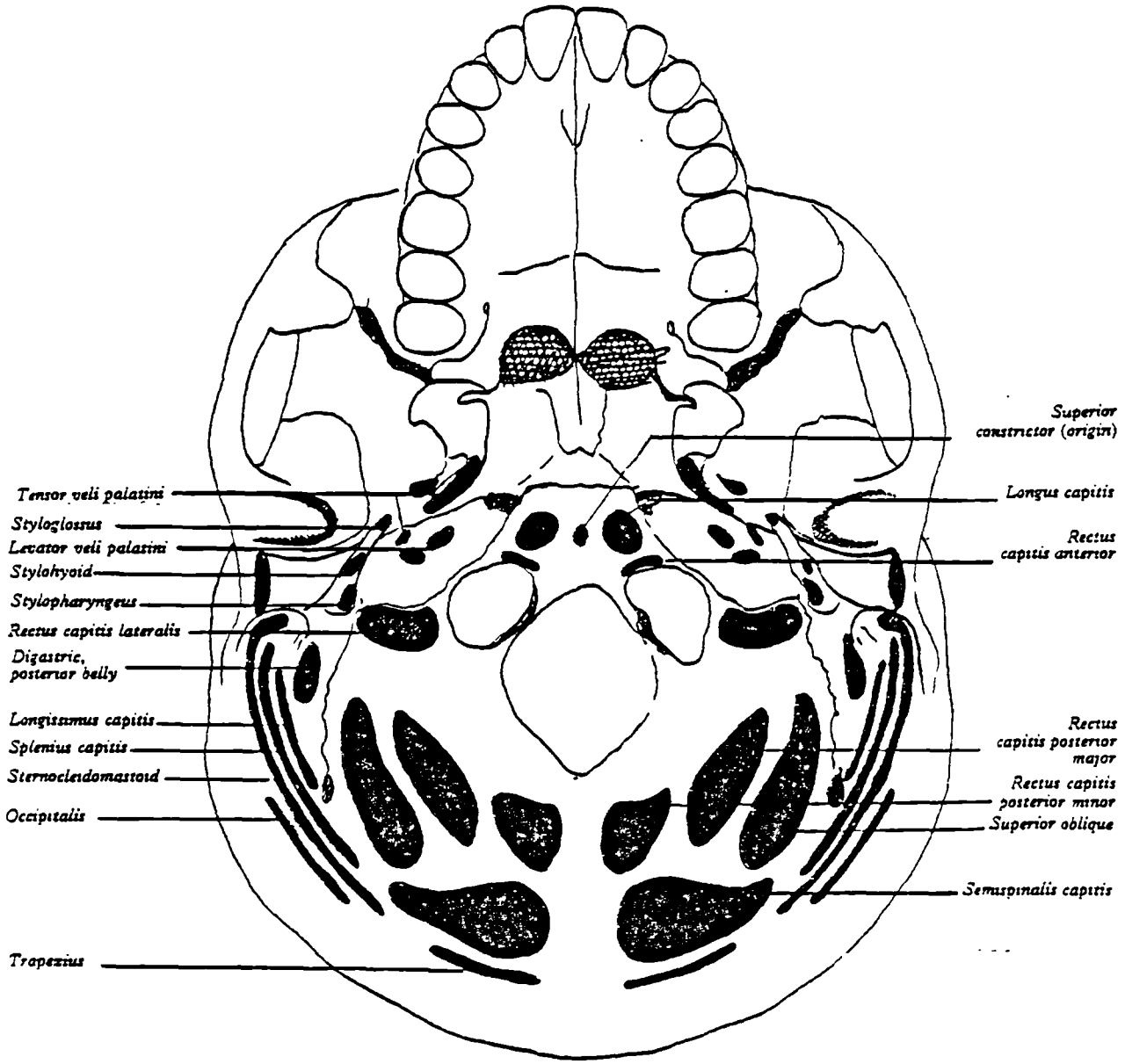
rectus capitis anterior major in the older literature). The former lies most posteriorly and arises from the anterior surface of the atlas, and passes obliquely upwards to be inserted into the basioccipital immediately anterior to the occipital condyles. In man it is usually separated from the muscle of the opposite side by about 1 cm. The longus capitis muscle is broad and thick and arises from the third, fourth, fifth and sixth cervical vertebrae. It converges towards its fellow of the opposite side and inserts immediately posterior to the superior constrictor of the pharynx. Its insertion is oval, the maximum diameter being about 1 cm. in the coronal plane. The attachments of these muscles on the human skull base are shown in the diagram Figure 4.

The literature concerned with details of muscle attachments to the cranial base in pongids is best dealt with in two sections, the first relating to the detailed anatomy of the prevertebral and upper pharyngeal musculature, and the second concerned with the musculature of the deep mastoid and nuchal regions.

Laitman et al, in their work on the relationship between basicranial anatomy and comparative anatomy of upper respiratory systems (1977, 1978 and 1979), claim that the exocranial orientation of the basicranium of extant primates is related to the position of upper respiratory structures such as the larynx and pharynx. However, these studies concentrate largely on the position of the larynx and no details of the musculature associated with the skull base region are given for the two dissected specimens of Pan troglodytes illustrated in Laitman (1977). Nonetheless, it is clear from this, and other descriptions which will be reviewed in this section, that the superior constrictor, tensor and levator palati muscles and the posterior belly of the digastric and muscles attached to the styloid apparatus in pongids all run in a direction more nearly parallel to the skull base than they do in man. Sonntag (1924) noted this and attributed it to prognathism of the jaws in the three great apes. Hill (1939) also

FIGURE 4.

Diagram of the human cranial base illustrating the areas associated with muscle attachments.



observed that in the Sumatran orang utan there was no Sinus of Morgagni as there is in man, the space between the superior constrictor and the cranial base being completely filled by the levator and tensor palati muscles. He also noted in the same specimen that the fibrous aponeurotic attachment of the pharyngeal 'vault' to the cranial base of the skull in this specimen was absent. This is, however, unlikely (Cave, personal communication) it being more probable that the height of the pharyngobasilar fascia is simply much reduced in the pongids.

Detailed descriptions of individual muscles from dissection accounts of the three great apes highlight several other differences from the anatomy found in modern humans. The close proximity of the pharyngeal and palatal muscles to the skull base has already been noted, but the generally much longer and drawn out skull base in the pongids means that the carotid canal, and the structures associated with the carotid sheath, no longer lie immediately lateral to the superior constrictor muscle. Instead, their medial relation in the pongids is the longus capitis muscle whose insertion in pongids extends further anteriorly than it does in humans. The area of insertion is larger than that in man, but the shape of the insertion is still oval; however, in pongids the maximum diameter lies in the sagittal plane. Raven (1950) and Bluntschli (1929) clearly demonstrate this in diagrams of their dissections of the gorilla and orang utan, and Hill (1939) noted that the thick fleshy bellies of the longus capitis create a deep groove on the posterior wall of the pharynx in the orang utan. It can also be seen from the diagrams of Raven and Bluntschli that the rectus capitis anterior muscles attach much closer to the midline in pongids, and Raven (1950) specifically mentions that the bellies are in contact with one another. The bony surface markings of these two pairs of prevertebral muscles are easily seen on dried pongid skulls, and they often extend close to the spheno-occipital synchondrosis.

The bony anatomy of the pongid cranial base in the region of the attachment of the tensor and levator palati muscles differ quite fundamentally from that of man. In the pongids both of these muscles are described as taking origin from the temporal bone, there being no mention of the tensor palati originating from the spine of the sphenoid or any such homologous structure on the sphenoid of the three great apes. Sonntag (1923), describing the dissection of a young female chimpanzee, notes that these two muscles have a strong common musculo-aponeurotic origin from the apex of the petrous temporalis bone, but he also states in a later paper that they may be fused or separate (Sonntag, 1924). Raven (1950) makes no mention of either of these two muscles in his report on the gorilla, but does show the stylohyoid arising from a 'processus styloideus' in the region of the petrous apex. Weidenreich (1951) observed that a similar process exists on gorilla skulls and originally termed it the "processus supratubalis" (1943), but later corrected this to "processus infratubalis" (1951), having first described such a process in crania attributed to Sinanthropus pekinensis (Weidenreich 1943). Zuckerman, Ashton and Pearson (1962) point out that where there is a 'petrous spine' in modern man "it is small and at the most gives attachment to some fibres of the levator palati muscle". Weidenreich (1951) dissected this region in a West African gorilla but found, contra to Zuckerman et al, that part of the tensor palati muscle took origin from the process. Broom (1950, p.21) regarded this same process in the fossil skull Sts. 5 as "apparently for the attachment of the levator palati muscle".

This process described in fossil hominids and extant hominoid crania is more correctly termed the 'eustachian process' (Owen, 1851) and is in fact present in most mammalian skulls (Cave, 1979). It is especially marked in the gorilla and in some chimpanzee skulls, but is less conspicuous in the orang utan. Cave (1979) describes this process as being exclusively occupied by the fibres of a ligamentous band, the mammalian temporo-pterygoid ligament. He also describes the mammalian tensor and levator palati

muscles as "arising contiguously (sometimes in common) from the caudo-lateral aspect of the cartilaginous part of the eustachian tube and adjacent undersurface of the cranial base, the medially situated levator muscle from the petrosal, the laterally situated and somewhat tendonous tensor muscle from the pterygoid process with occasional extension onto the petrosal". Cave gives detailed descriptions of dissections of this region in Pan, Gorilla and Pongo which support such an arrangement of these structures in the pongids (as well as in many other mammals).

Thus, from these accounts, the stylohyoid, the tensor and levator palati muscles and the temporo-pterygoid ligament have all been described as taking origin from the eustachian process. It is interesting to note that Doyle and Rood (1979) also noticed a large series of fascial thickenings between the medial pterygoid and the tensor palati muscles in the macaque. They suggested that these may be 'check ligaments', representing a more direct association between these two muscles.

Zuckerman et al (1962) point out that an ossified styloid process is a constant feature of the adult human skull. In adult chimpanzees and gorillas a completely ossified styloid process is seldom found because its cartilaginous connection with the petrous temporal bone means that it is usually lost when the skull is macerated. Nonetheless, the authors claim that a short, ossified styloid process may be found in some 50% of adult orang utans, even after the skull has been macerated. However, even when the process itself is lost, the position is marked by a pit. Zuckerman et al (1962) dissected several primates including one chimpanzee and one orang utan. They concluded that, although in the apes the styloid may be cartilaginous or ligamentous, its muscular attachments are the same as those in man. They noted, however, that in the chimpanzee, unlike man and the orang utan, the stylomandibular ligament gains attachment to the vaginal process of the tympanic and not to the styloid process itself. Where the styloid muscles of pongids are mentioned in the literature, e.g. Sonntag

(1923, 1924), their cranial attachments are described as being identical to those of man. Sonntag (1924) did, however, note that in the orang utan the stylohyoid usually runs to the wall of the air sac, so forming a stylolaryngeus, but that it can also occasionally form a 'true' stylohyoid.

The mastoid, nuchal and deep nuchal musculature of the Pan, Gorilla and Pongo also show differences in their cranial attachments when compared to those of modern man. Recently, considerable attention has been attached to what are thought to be the bony markings corresponding to the attachment of the posterior belly of the digastric on the skull base of the pongid and fossil hominids (Olson, 1978). The digastric fossa in man is deep and narrow, and between this fossa or groove, and the groove for the occipital artery, there is in the majority of modern human crania a crest known as the juxtamastoid process (Walensky, 1964). The incidence, size and relationships of this eminence in crania of modern man have been investigated by Taxman (1963) and Walensky (1964). Taxman found that it was present in 89% of a series of 400 modern crania. He also investigated the relationship of the digastric muscle to this eminence and found that the posterior belly of the digastric muscle not only arose from the floor of the mastoid notch, as normally described in anatomy texts, but was also, and sometimes mainly, attached to the juxtamastoid eminence. This suggests that the development of the juxtamastcid eminence might be related to the attachment of the posterior belly of the digastric. In any case, it demonstrates that this muscle does not bear the sort of discrete relationship to the digastric or mastoid notch that is implied in modern anatomical texts. Walensky suggests that there is a gradual transition from the small mastoid process, wide digastric fossa and raised occipitomastoid suture (occipitomastoid crest) present in early human crania, to the features characteristic of modern human crania. This generalized modern human pattern consists of a large mastoid process, a narrow digastric fossa bounded by a marked juxtamastoid process which separates it from the groove for the

occipital artery; the occipitomastoid suture being flattened, with no occipitomastoid crest. Olson (1978) states that "in the extant pongids the digastric muscle has a non-linear ovoid origin on the medial surface of the occipitomastoid crest, immediately lateral to the groove for the occipital artery". Raven (1950) shows the origin of this muscle in the gorilla placed centrally over the occipitomastoid suture immediately posterolateral to the rectus capitis lateralis, with no indication of an associated groove or tubercle marking its origin. This also appears to be the case in the orang utan (Bluntschli, 1929) and in the macaque; Schwarz and Huelke (1963) have specifically stated that "no fossa or tubercle marks the origin of the posterior belly of the digastric". Sonntag (1923), however, considers that in the chimpanzee the posterior belly of the digastric arises from a depression on the temporal bone corresponding to the digastric fossa in man. It is also worth noting that Sonntag (1924) describes the occipital artery in the chimpanzee as arising from the beginning of the external carotid and running upwards and backwards under the sternocleidomastoid and splenius to end among the muscles of the neck. He makes no mention of it grooving the occipital bone in any of the three great apes. Sakka (1977) provides additional details for the origin of the posterior belly of the digastric in hominoids. He reports that in Gorilla the digastric is extremely powerful, the cranial insertion being wide and posteriorly positioned, situated lateral to the anterior part of the superior oblique. In contrast, the origin of the posterior belly of the digastric in Pan is less extensive and tends to be placed more anteriorly, which is reflected in its relation to the insertion of the superior oblique. In man, Sakka describes both the superior oblique and the posterior belly of the digastric as being considerably reduced in size with a more anteriorly situated attachment which has migrated laterally nearer to the mastoid process. Sakka adds that the anterior migrations of the digastric and superior oblique are in keeping with changes in the poise and carriage of the head. Lateral and posterior to the digastric muscle

and deep to the splenius and sternomastoid muscles in man, the longissimus capitis or trachelomastoid inserts into the posterior margin of the mastoid process. Raven (1950) shows this muscle as having a similar insertion in Gorilla posterolateral to the digastric, and deep to the cleidomastoid part of the sternocleidomastoid. The longissimus capitis leaves no bony marking on the human skull base, but so far as can be determined from the diagrams of Raven and Bluntschli, it may occupy a shallow groove just lateral to the crest which marks the border of the superior oblique muscle in pongids.

CHAPTER 4.

The cranial base of fossil hominids.

Hominid phylogeny and classification have always concentrated on features of the neurocranium, facial skeleton and dentition. The anatomical complexity of the cranial base, together with the fact that functions of mastication, respiration and balance are all intimately associated with it, may have deterred attempts to integrate morphological features of this region into phylogenetic and functional models of hominid evolution. Detailed studies of the cranial base of fossil hominids are usually part of broader contributions to the comparative anatomy of either individual crania (Tobias, 1967; Clarke, 1977) or groups of related crania (Weidenreich, 1943, 1951; DuBrul, 1977). Other studies have been specifically concerned with the position of the foramen magnum and occipital condyles and the orientation of the nuchal plane (Le Gros Clark, 1950; Ashton and Zuckerman, 1951, 1956(a); Moore et al, 1973; Adams and Moore, 1975). The reconstruction of the relationship of soft tissue structures of the upper pharyngeal region to the cranial base has also formed the basis of another functional research approach (Lieberman and Crelin, 1971; Laitman, 1977; Laitman et al, 1979; Sakka, 1977).

Dart (1925) was the first to draw attention to the fact that the foramen magnum and occipital condyles are relatively further forward in position on the skull base of Australopithecus africanus than they are in the extant pongids. Since then, others, e.g. Sergi (1930); Weidenreich (1943, 1951); Ashton and Zuckerman (1951, 1952); Le Gros Clark (1971), have confirmed that this is also the case in A. africanus, A. robustus, Homo erectus and neanderthal crania. One way of quantifying this is by expressing the position of the occipital condyles as a percentage distance along a line drawn from opisthocranion to prosthion parallel with the Frankfurt Horizontal. Comparisons of this type are obviously influenced by the degree of progna-

thism and the size of the nuchal crest. The position of the occipital condyles relative to the biporial axis, however, is independent of these differences, and Tobias (1967) points out that both the 'gracile' and 'robust' australopithecines' skulls, Sts 5 and OH 5 have condyles that lie on the biporial axis despite the fact that they show differences in the condylar index. Ashton and Zuckerman (1956,b) also note that the line joining the tips of the mastoid processes passes well posterior to the occipital condyles in the 'robust' cranium SK 47, whereas in modern man it passes only just posterior to the middle of the occipital condyles, implying that the condyles are even more forward in this 'robust' australopithecine specimen than in man when measured in this way. Broom and Schepers (1946, p.123) have also stated that the foramen magnum is "farther back in Plesianthropus than in Paranthropus" and that "the distance from the foramen magnum to the foramen ovale in Plesianthropus is 33 mm. and in Paranthropus about 26 mm.", adding that "probably Paranthropus walked even more erect than Plesianthropus".

There is little information about the degree of endocranial skull base flexion in fossil hominids. Weidenreich (1947) notes that the entire problem of skull base flexion and its correlation with the degree of prognathism had fallen out of favour, although it had been the subject of study 80 years previously. This was partly because of the complete lack of fossil hominids with preservation of the "basilar parts of the skull". Weidenreich points out, however, that all the neanderthal fossils possess a greater angle of skull base flexion than modern man and "in the Homo soloensis skull the basilar angle - difficult to determine exactly by any method - comes close to 160^{o}". He adds, "a line from the foramen caecum to the tuberculum sellae turns downwards towards the dorsum sellae whence it runs along the clivus to the foramen occipitale .... this angle is about 140^{o} in Solo man". Later (1951, p.283) Weidenreich states that "the most characteristic feature of the

(Solo) skulls is the flatness of the base as compared with that of modern man", the reason being "that the posterior fossa itself is not only much flatter than in modern man, but also descends much less". (It is worth noting that Washburn and Howell (1952) considered that Weidenreich mistook the sphenoidal sinus for the pituitary fossa in the Homo soloensis skull XI, so that the estimates for the angle of cranial base flexion may be in excess of the true values.) Weidenreich (1947) concludes that "it is easy to recognize the direct correlation between the prolongation of the base and the growth of the jaws" in the anthropoids, and the "close resemblance between juvenile anthropoids on one hand and early and modern man on the other". Ashton, Flinn and Moore (1975) have measured the spheno-ethmoidal and foraminobasal angles of Sts 5 and OH 5 using the midsagittal craniograms published by Tobias (1967). These are given as being, respectively, 129^{o} and 109^{o} for Sts 5 and 121^{o} and 128^{o} for OH 5. Ashton et al use the definition of nasion given by Ashton (1957) and employ prosphenion, endobasion and opisthion as the landmarks for these angles. They conclude that the fossils "emerge as distinct from all living genera and from each other". The values for the spheno-ethmoidal angles given in the study of Ashton et al suggest that both Sts 5 and OH 5 are more flexed than the modern human skull, but re-examination of figures in Tobias (1967) suggest that the true values are near 145^{o} and 140^{o} when nasion is used. However, the nasion (in Tobias, 1967) does not lie in the same horizontal plane as the sella-foramen caecum line and when the angle basion-sella-foramen caecum is estimated from these craniograms, they are 138^{o} and 130^{o} respectively. The values for the foraminobasal angle in Sts 5 (109^{o}) and OH 5 (128^{o}) given by Ashton et al (1975) also differ from those published by Tobias (1967, p.47) where the "angle opisthion-basion-prosthenion (OBP)" is given as 113^{o} in Sts 5 and 126^{o} in OH 5, but the differences are minor ones. Tobias (1967, p.46) shows that the foramen magnum in OH 5 is more horizontal than that in Sts 5; however, both are nearer to the horizontal than is the plane of the foramen

magnum in extant pongids. Tobias draws attention to the fact that the foraminobasal angle, often used to measure this inclination, is also influenced by endocranial skull base flexion which raises the prosphenion. The more forward inclination of the foramen magnum tends to open out the angle and the endocranial base flexion tends to close it, so that when they occur together during 'hominisation', they act to cancel out any change in the foraminobasal angle.

The presumption that the position of the foramen magnum and the foraminobasal angle are posture related has already been discussed in Chapter 2, but DuBrul has extended this argument by discussing the differences in the degree of adaptation to bipedalism when the proportions of the face and neurocranium are very different. DuBrul (1977) has assumed that both the 'gracile' and 'robust' forms of Australopithecus were bipedal, but that the degree of adaptation was not the same in the two taxa. Because of the massively heavy face of the 'robust' australopithecines, difficulty in balancing the head on the vertebral column has been overcome by a combination of severe 'buckling' of the cranial base at the sella, a shortening of the cranial base, and an anterior shift in the position of the foramen magnum and occipital condyles and the swinging down of the nuchal plane. He also comments that there has been a strong retrusion of the facial complex as well as an inward rotation of the petrous pyramids as a result of basal compression. The lighter, more easily balanced 'gracile' skull shows some of these modifications, but not so marked as those occurring in the heavy 'robust' skulls. The skull base shows much less endocranial skull base flexion, more sagittally orientated petrous pyramids, some prognathism and less forward shift in the position of the foramen magnum and occipital condyles. Björk (1950) has argued (see Chapter 1) that the degree of cranial base flexion in the anthropoids results from a compensatory backward growth in response to the massive protrusive growth of the jaws. The intermediate degree of prognathism and skull base flexion in the 'gracile' australo-

pithecines when compared to the pongids and modern man would fit in with this thesis. In the 'robust' australopithecines the masticatory adaptations such as widening of the jaws and an increase in the height of the ramus have resulted in a longer and wider but less prognathous face. Thus, the degree of skull base flexion might still bear some relationship to the degree of prognathism in these fossil hominids. These studies draw attention to the complex interaction of facial and neurocranial changes that can influence the cranial base, and the care with which angles and measurements should be interpreted in comparative studies.

DuBrul's observations about the petrous axes in the 'robust' and 'gracile' australopithecines supplement the detailed description of the temporal bones in Sinanthropus pekinensis that Weidenreich (1943) gave. Weidenreich noted that in modern man a line drawn through the axes of the petrous pyramid and tympanic plate formed a straight line passing through the carotid canal. In Sinanthropus these axes form an angle, the vertex of which coincides with the carotid canal. Weidenreich (1943) gives the "deviation angle of the pyramid axis" to the midline as 63^{o} in one European skull, 40^{o} in Sinanthropus, 15^{o} in a gorilla skull and 30^{o} in a single orang utan skull, but these data obviously give no indication of the variation within each taxa. Weidenreich sttributes the condition in modern man to the more transverse orientation of the petrous axis, and not to any alteration in the tympanic axis. He states that the change in the petrous axis is due to a shortening of the basioccipital and length of the petrous pyramid following a 'rolling up' of the brain-case about a transverse axis which runs from one portion to the other.

Tobias (1967, p.33) lists the angle between the tympanic and petrous axes as 60^{o} - 73^{o} in a small sample of Gorilla, 53^{o} - 75^{o} in a small sample Pan and 55^{o} - 58^{o} in Pongo. He reports the angle for OH5 as 30^{o} - 35^{o}, and thus well outside the pongid range. Tobias remarks that both Paranthropus and Australopithecus are intermediate between pongids and modern

man in the orientation of the petrous bones, but closer to the value in modern man. Clarke (1977, p.262) notes that the tympanic and petrous axes in SK 847 are similar in orientation to that of Homo sapiens. Clarke also draws attention to the supposed Australopithecus cranial base Sts 19. This was discovered in one of the 'dumps' of rubble (Broom et al, 1950, p.27-33) and may possibly be from Member 5 of the Sterkfontein formation, in which case it would be the same stratigraphic horizon that yielded the early Homo cranium, Stw 53 (Hughes and Tobias, 1977). Clarke states "so different is Sts 19 from the more chimpanzee-like Sts 5 that the possibility that Sts 19 is an early Homo cranium has to be considered". The posterior endocranial surface of the petrous temporal in Sts 19 is vertical and reminiscent of that in modern man (and of SK 847). However, according to Clarke, the degree of angulation of the petrous axis in Sts 19 follows the pattern observed in the 'gracile' australopithecines. Broom et al (1950, pl.2) considered the endocranial cast of Sts 19 as of a highly advanced type, noting that "the manner in which the cerebellum has come to be shifted forward and below the cerebral occiput is most striking". Clarke (1977, p.260) tentatively suggests that this may be associated with the more vertical posterior surface of the petrous temporal bone and that there may be "an evolutionary correlation between the downward and forward movement of the nuchal plane and foramen magnum and the corresponding downward and forward movement of the cerebellum". Tobias (1967) and DuBrul (1977) both draw attention to the marked downward displacement of the nuchal plane in the OH 5 cranium to below the Frankfurt Horizontal. DuBrul considers that this accompanies the rotation of the petrous pyramids in the 'robust' australopithecines. Leakey, Mungai and Walker (1971) have, however, commented upon the rather steep angle the nuchal plane makes with the Frankfurt Horizontal in another 'robust' cranium, KNM ER 406, which nonetheless shares with OH 5 the same inward rotation of the petrous axes (Dean and Wood, 1981,a). Whatever the relationship between the nuchal

plane, cerebellum and petrous pyramids it seems likely that it is a complicated one.

Weidenreich's comparative studies have drawn attention to another important feature of the hominid cranial base, the length of the tympanic plate. In pongids the length of the tympanic plate is greater than the exposed portion of the petrous temporal bone, whereas in modern man the reverse is true (Weidenreich, 1951). The fact that the length of the tympanic plate differs in male and female gorillas led Weidenreich to suppose that this was not related to auditory function, but to the development of the masticatory apparatus.

Clarke (1977) developed the transverse mastoid-occipital index to express the relationship of the mastoid breadth to the total bioccipital breadth. In the index the breadth of the mastoid portion of the temporal from the occipitomastoid suture to the most lateral part of the mastoid process is expressed in terms of the distance from the occipitomastoid suture to the lateral margin of the foramen magnum. Mean values of the index ranged from 74 for modern man to 185 for male chimpanzees. Thus, pongids have a broad mastoid and long tympanic plate whereas Homo sapiens has a long mastoid and a short tympanic plate. This suggests that there is a correlation between length of the tympanic plate and breadth of the mastoid region. Clarke goes on to point out that this relationship also holds good for fossil hominids where a broad mastoid region always accompanies a long tympanic plate. Thus, the studies of Weidenreich and Clarke suggest that the length of the tympanic plate is influenced by both masticatory adaptations and the width of the mastoid region of the temporal bone.

Perhaps understandably, few studies of the cranial base of fossil hominids have attempted to reconstruct the soft tissues of the pharynx and upper respiratory tract. Notable exceptions are the studies of Lieberman and Crelin (1971), Laitman (1977) and Laitman et al (1979) in which the authors

have set out to reconstruct the shape of the upper respiratory tract in fossil hominids. Leiberman and Crelin (1971) examined the cranial bases of infant human, adult chimpanzee and neanderthal skulls and on this evidence concluded that neanderthal man could not have possessed human speech abilities. This study has been severely criticised on several grounds. These vary from the use of the styloid process to reconstruct the position of the larynx, to the authors' deviation from the more usual approach to the problem of the origin of language that proposes that cerebral reorganisation underlies speech capability. Followers of this theory suggest that the vocal tract of primates was preadapted for speech long before the emergence of Homo sapiens (Wind, 1978). Laitman investigated the cranial base of fossil hominids by using the relationship of exocranial skull base flexion with the known position of upper respiratory structures in extant primates. Using this model, Laitman (1977) concluded that the great similarity in exocranial skull base flexion between the australopithecine, Sts 5, and extant pongids indicated that "Sterkfontein 5 probably had a tongue which lay entirely within the oral cavity, with no portion forming an anterior aspect of the pharynx. Its hyoid and associated infra- and supra-hyoid muscles were also likely positioned high in the neck. Correspondingly, the larynx would have been positioned high, probably lying opposite the first and fourth cervical vertebrae. This high position would permit an intra-narial epiglottis to be present and thus the possibility of a nasopharyngeal-laryngeal airway during the ingestion of a bolus of liquid. As with extant non-human primates, Sterkfontein and other australopithecines were most probably obligate nose breathers, maintaining a patent nasopharyngeal-laryngeal airway during quiet respiration, ... the range of vocalisation of Sts 5 was thus probably not considerably greater than that shown by present day pongids". Laitman does not give information about any other Plio-Pleistocene fossil hominids, but does provide data for a group of European neanderthals (including La Ferrassie, Monte Circeo and Saccopastore). These,

while not being identical to either adult or subadult modern humans, he concluded, are considerably different in their upper respiratory structure and function from the more pongid-like australopithecines. Other fossil skulls (including Cro-Magnon, Steinheim and Broken Hill) were claimed to have possessed a structural arrangement of the upper respiratory system which closely resembled that of mature modern humans. However, Proffitt, McGlone and Barrett (1975) have shown that in modern man the height of the oropharyngeal cavity is closely related to the length of the neck and, as a result, to the proportion of the tongue present in the oral cavity. Proffitt et al demonstrated that the short neck of the Australian aborigine is associated with a small oropharyngeal cavity. As a result of this oropharyngeal reduction, the "more forward and higher resting position of the tongue" has contributed to the expanded dimensions of the oral cavity and so may in part account for the increased size of the dental arches and jaws in the Australian aborigine. Mention has already been made of several authors, e.g. Huxley (1863, 1867), Sonntag (1924), Weidenreich (1947) and Björk (1950) who considered cranial base flexion to be closely related to the size of the jaws, and in the light of variations in the basicranial anatomy of early fossil hominids reported by other authors, e.g. DuBrul (1977), Clarke (1977) and Dean and Wood (1981,a), Laitman's conclusions regarding early fossil hominids (based upon one cast of Sts 5) cannot be regarded as representative of all australopithecines.

Many descriptive studies of fossil hominids discuss details of muscle markings in the region of the skull base. Differences between the major groups of fossils are most easily summarised by considering first the prevertebral muscle markings, then the markings in the region of the digastric groove, and finally the markings of the nuchal muscles.

The prevertebral muscle markings in crania belonging to Australopithecus africanus are particularly distinct. Broom, Robinson and Schepers (1950) drew attention to the marked elevations on the basioccipital,

"presumably for the rectus capitus anticus muscles". These are present on Sts 5, MLD 37/38 and, to a lesser extent, on Sts 19. The 'gracile' australopithecines also have a well formed eustachian process on the underside of the apices of the petrous temporal bones, which Broom et al considered marked the attachment of the levator palati muscle (see Chapter 3). These two features do not seem to occur to the same degree, if at all, in the 'robust' australopithecines (Tobias, 1967 and Leakey et al, 1971) but Weidenreich (1943, 1950) does draw attention to a eustachian process, called by him the 'processus supratubalis' (1943) and 'processus infratubalis' (1950) in Homo erectus (a similar, but smaller, process is also present on the OH 24 cranium and cranium TM 1517 from Kromdrai - see later).

Broom et al (1950) describe the attachment of the digastric muscle to the mastoid region of the skull base in the 'gracile' australopithecine skull Sts 19, as being to a "deep wide digastric fossa which is continued back to the sloping and smooth back part of the mastoid region". Tobias (1967) also describes the attachment of the posterior belly of the digastric muscle to a fossa in OH 5 as "exactly" like that of modern man. Ashton and Zuckerman (1956,b) noted a "sharp digastric groove" in the 'robust' cranium SK 47, with a well marked groove "apparently for the occipital artery" running parallel to its anterior half. Sakka (1977) examined the 'robust' australopithecine cranium KNM ER 406 and describes the origin of the superior oblique muscle as large, elongated and "comma-shaped", directed upwards and backwards almost to the superior nuchal line, tne digastric muscle being situated lateral and anterior to the muscle encroaching widely and posteriorly. Olson (1978), however, quotes Sakka as "reporting a linear origin for the digastric muscle from a sulcus on the right hand side of the planum nuchale". Olson considers that this sulcus is a "posterior continuation of the occipital groove at the point just prior to where the (occipital) artery pierces the nuchal fascia connecting the sternocleidomastoid and trapezius muscles, tne

digastric muscle originating lateral to this groove". Leakey et al (1971, 1972) also describe this as a groove for the occipital artery in the 'robust' Australopithecus crania KNM ER 406 and KNM ER 407, but Clarke (1977) considers that the same groove is "more likely the site of attachment of the superior oblique muscle" in these fossils. Weidenreich (1943, p.63) notes that there is "no essential difference between the general character of the digastric fossa between Sinanthropus and modern man". None of these descriptions of the posterior origin of the digastric muscle in fossil hominids suggests that the insertion in the fossils resembles the wide, oval origin such as that found in the pongids.

Ashton and Zuckerman (1956,b) describe the muscle markings of the occipital region of SK 47 as being "generally more pronounced than in man but not more so than the gorilla" and that the attachments for the semispinalis, rectus capitus posterior major and rectus capitus posterior minor are "easily made out". Leakey et al (1971) also state that the markings for the nuchal muscles in KNM ER 406 are clearly marked. They go on to say that the attachment areas for the semispinalis capitis and superior oblique taken together are much greater than the common area for the two parts of the rectus capitus posterior muscle. Clarke (1977) provides more details for the 'robust' cranium SK 47, and describes a "spatulate shallow depression on the occipital bone for the attachment of the superior oblique muscle immediately medial to the occipitomastoid crest and bounded medially by a slight crest similar to that seen on the left side of OH 5". Clarke considers that the crest is developed to provide extra attachment for the superior oblique muscle.

Tobias (1967) describes a pronounced external occipital protuberance in OH 5, which he considers as being for the attachment of a well developed ligamentum nuchae. He regards the strong development of this ligament in OH 5 as indicative of a poorly balanced head that tended to incline forwards. Leakey et al (1971), however, have remarked that the external occipital protuberance in KNM ER 406 is "not as greatly developed as might be expected

from the massive build of the cranium". This suggests that there is a great deal of variation in the development of the external occipital protuberance in the 'robust' australopithecines. There is even less indication of an external occipital protuberance, and thus of a ligamentum nuchae, in the 'gracile' australopithecines as far as can be determined from the descriptions and illustrations given by Broom et al (1950) for the Sterkfontein crania and Dart (1962) for MLD 37/38. Adams and Moore (1975) have extended these qualitative observations of muscle markings and have measured the area of attachment of the nuchal muscles. The authors used a planimeter and projected negatives of photographs taken perpendicular to the nuchal plane of skulls of Homo sapiens, Pan and Gorilla, as well as casts of Sts 5 and OH 5. They found that the area was greater in Gorilla than in Pan, with Homo sapiens falling between the two. The nuchal area of OH 5 was within the range of modern Homo sapiens while that for Sts 5 was much smaller, falling below the range for Pan troglodytes.

PART II MATERIALS AND METHODS.

Chapter 5. Materials.

Chapter 6. Methods.

Chapter 7. Method of ageing individual skulls.

CHAPTER 5.

Materials.

The materials used in this thesis consisted of a large comparative sample of extant primate taxa (both skulls and wet specimens suitable for dissection) and several fossil hominid crania . The majority of the fossils were original specimens and the remainder were examined by means of casts.

Comparative sample

The comparative sample was made up of specimens of Homo sapiens, Gorilla gorilla, Pan troglodytes and Pongo pygmaeus. These taxa were selected for the following reasons:

(i) The balance of molecular and other comparative anatomical evidence suggests that the three great apes and modern man are more closely related to early fossil hominids than any other extant primates, and so can be expected to provide useful information such as the possible range of variation within fossil taxa.

(ii) For the same reasons, closely related extant taxa should provide the most suitable data base to assess the significance of differences between early fossil hominid crania.

(iii) Sufficient numbers of skulls of these taxa exist in museum and medical school collections to enable reasonable and reliable estimates of population parameters to be made.

(iv) Juvenile skulls of all four taxa are included in such collections, so that additional data about growth changes could also be collected.

Details of the skulls of adult and juvenile specimens of Homo sapiens, Gorilla gorilla, Pan troglodytes and Pongo pygmaeus appear in Tables 1 and 2 at the end of this section, and the fossil hominids used in this study are listed in Table 3. All this material, and the wet specimens used in the

dissection study are described below. The catalogue numbers of the specimens, together with the case numbers allocated to them, appear in Appendix 1. The definitions of adult and juvenile skulls used in this thesis are given in Chapter 7.

Homo sapiens

Adults

Thirty skulls of unknown sex and mixed race were measured. These were taken from the teaching collection of the Department of Anatomy, The Middlesex Hospital Medical School.

Juveniles

Fifty juvenile specimens of Homo sapiens were used, made up of skulls from four collections. These included 14 skulls from the teaching collection of the Dental Anatomy Department, University College, London; 10 skulls from the Osman Hill Collection kept in the Osteology Department of the British Museum (Natural History), London; 19 skulls from the Odontological Museum, The Royal College of Surgeons of England, London; and 7 skulls from the teaching collection of the Anatomy Department, The Middlesex Hospital Medical School, London.

Gorilla gorilla

Adults

Thirty specimens, made up of 15 males and 15 females, were used in the study. Four males and one female were from the collection housed at the Powell-Cotton Museum, Birchington, Kent and the remaining 25 specimens were from the collection in the Primate Department of the British Museum (Natural History), London.

Juveniles

Fifty-nine juvenile specimens of Gorilla gorilla were used in this study; 27 from the Primate collection of the British Museum (Natural History) and 32 from the Powell-Cotton Museum, Birchington, Kent,

Wet specimens

Two specimens of Gorilla gorilla were used in the dissection study. Both were kindly made available by the Curators of the Osman Hill Collection, The Royal College of Surgeons of England, Lincoln's Inn Fields, London. Originally preserved in formalin, these two heads had completely dried out and were immersed in 2% formalin solution to recondition the soft tissues that remained in the region of the skull base.

The first specimen was a juvenile of indeterminate sex with completely erupted deciduous dentition. The head had been severed from the neck through the atlanto-occipital joint and there was considerable damage to the soft tissues in the region of the insertion of the prevertebral muscles to the skull base.

The second specimen was a juvenile female with completely erupted deciduous dentition and fully erupted first molars. The head had also been disarticulated from the cervical spine at the atlanto-occipital joint but in this case, the head was also trephined in the mid-sagittal plane. The prevertebral and upper pharyngeal muscles were also damaged in this specimen.

Pan troglodytes

Adults

Thirty specimens, 13 females and 17 males, were used in the study. Seven of the female specimens were from the collection at the Powell-Cotton Museum, Birchington, Kent and the remaining 23 specimens were taken from the Primate collection of the British Museum (Natural History), London.

Juveniles

Sixty-eight juvenile specimens of Pan troglodytes were used in this study. Thirty-two were from the Primate collection of the British Museum (Natural History), London and 27 from the Powell-Cotton Museum, Birchington, Kent.

Wet specimens

Two specimens of Pan troglodytes were used in this study. The first, a juvenile specimen with an incompletely erupted deciduous dentition, was purchased from the London Zoological Society by the Department of Dental Anatomy, University College, London and was generously made available for dissection by Professor A. Boyde. The specimen consisted of the head only, disarticulated from the cervical vertebrae at the level of C_1 and C_2, and the left mandibular ramus and the left side of the mandibular body was missing. This specimen had been preserved in formalin for some time.

The second specimen of Pan troglodytes was made available for dissection by courtesy of the Department of Mammals of the British Museum (Natural History), London. The animal, a mature male, had been raised in captivity and destroyed on becoming aggressive and difficult to manage. This specimen was preserved in formalin solution. The larynx and some structures of the lower pharynx had been removed at a post mortem examination.

Pongo pygmaeus

Adults

Thirty specimens, 17 males and 13 females, were used in the study. One male and four female specimens were from the collection in the Odontological Museum, The Royal College of Surgeons of England, Lincoln's Inn Fields, London and the remaining 25 specimens from the Primate collection of the British Museum (Natural History), London.

Juveniles

Forty-three juvenile specimens of Pongo pygmaeus were used in this study; 27 from the primate collection of the British Museum (Natural History), London; 11 from the teaching collection of the Dental Anatomy Department, University College, London; and 5 from the Odontological Museum, The Royal College of Surgeons of England, London.

Wet specimens

A single adult male specimen was made available for dissection by the Department of Mammals of the British Museum (Natural History), London. This animal, originally reared by the London Zoological Society, was skilfully embalmed in preparation for dissection by Mr. A. Rote and Mr. S. Karby of the Department of Anatomy, The Middlesex Hospital Medical School, London. At the time of embalming, a quantity of red resin was introduced into the right common carotid artery in an attempt to make the identification of arteries in the head and neck easier during the dissection.

Criteria for inclusion of individual specimens

Specimens of dried skulls were included in the sample provided they satisfied the following criteria.

1. There was no evidence of significant distortion or damage to the cranial base, or to any of the landmarks used in the study.
2. There was no evidence of pathology in either the skull, or developing dentition.
3. In the case of adult specimens of Gorilla gorilla, Pan troglodytes and Pongo pygmaeus it was possible to sex the skull either from Museum records or direct examination. (The Homo sapiens sample and the juvenile pongids were not sexed.)
4. That there was no ambiguity as to the identity of any juvenile or adult skull.

Great ape material suitable for dissection is extremely difficult to obtain, and any suitable material or any specimens which could be rehydrated, were included in this study.

Fossil hominids

Early fossil hominid crania, and casts of fossil hominids from East and South Africa, were included in the study, and details of this material appear below. A list of the casts and original specimens appears in Table 4 at the

end of this chapter.

Criteria for inclusion of individual specimens of early fossil hominids

Every effort was made to include all the available original specimens of fossil hominids from East and South Africa in which it was known that the basicranium was either complete, or partially preserved. Particular emphasis was laid on the inclusion of specimens preserving all of the cranial base region, but rather than exclude partially preserved and damaged specimens, it was considered more useful to reconstruct the probable position of the basicranial landmarks used in this study - (see Chapter 6, Section ix). In the few cases in which it was not possible to examine original specimens, it was decided to include measurements made from casts of the originals rather than omit data from these specimens altogether.

Original specimens were kindly made available for study by the Directors of the National Museums of Kenya, Nairobi, Kenya; the Transvaal Museum, Pretoria, South Africa; and the Department of Anatomy, University of Witwatersrand, Johannesburg, South Africa. The final total of original early fossil hominid specimens included in this study was 17, and two casts of specimens from Olduvai Gorge, Tanzania, were also included.

To supplement the metrical analysis of the cranial base, eight of the more complete specimens were chosen and plaster casts of the cranial base region were made using existing fibreglass casts of the original specimens as templates. These duplicate plaster casts were used to study muscle markings on the cranial base - (see Chapter 6, Section x). The specimens used in this part of the study included: MLD 37/38, Sts 5, SK 47, OH 24, KNM-ER 406, 407, 1805, 1813 and OH 5.

The condition of the fossil hominid specimens used in this study

The fossil hominids chosen for this study are not equally well preserved. Five of the more complete specimens (KNM-ER 406, KNM-ER 3733, KNM-ER

3883, OH 5 and Sts 5) are sufficiently well preserved and undistorted to identify all the landmarks defined in part ii of the section on Methods, and it was possible to make reliable estimates of all the measurements on these crania.

Three of the crania (Sts 19, MLD 37/38 and SK 47) are damaged in the region of the infratemporal fossa. The cranial base of Sts 19 is mostly complete and undistorted and, of the landmarks used in this study, only the right infratemporal crest is damaged. The left infratemporal crests of both MLD 37/38 and SK 47 are damaged but, apart from this, both crania are well preserved and undistorted in all regions of the cranial base. Five specimens (KNM-ER 407, 1470, 1805, 1813 and OH 9) are damaged in the region of the basioccipital and/or the foramen magnum. KNM-ER 407 is preserved in the region of the foramen magnum but parts of the sphenoid bone anterior to the spheno-occipital synchondrosis are either missing or damaged; the right and left infratemporal crests in this specimen are preserved. The cranial base of KNM-ER 1470 is badly damaged and interpretation of the base is further complicated by distortion. However, estimates of the following landmarks can be made: the infratemporal crests, the lateral extremities of the tympanic plates, the foramina ovale and part of the right carotid canal. Specimens KNM-ER 1805, 1813 and OH 9 are all damaged in the region of the foramen magnum and the basioccipital. In specimens KNM-ER 1805 and 1813, the basioccipital is completely missing but in OH 9 parts of the basioccipital are present and it is possible to make some estimate of the probable position of the foramen magnum.

The cranium OH 24 was found in a badly distorted state, embedded in a mass of calcareous matrix, but many of the pieces of the crushed skull have been separated, cleaned and reassembled (M.D. Leakey, Clarke and L.S.B. Leakey, 1971). Despite this extensive and skilled attempt at restoration, the cranium remains slightly distorted and the right petrous and tympanic plate are still in their crushed position. There has also been some recon-

struction of the lateral end of the left tympanic plate.

Five crania (KNM-ER 732, Sts 25, SK 847, TM 1517 and Taung) are complete on one side only. KNM-ER 732 is preserved only on the right hand side. The following landmarks, however, can be identified; the lateral extremity of the right tympanic plate, the right carotid canal, and the position of the right petrous apex. The right infratemporal crest can also be estimated to within a few millimetres. Sts 25 is preserved only on the left hand side. The petrous apex, carotid canal and lateral extremity of the tympanic plate are preserved and the position of the infratemporal crest can also be estimated. The cranial base of SK 847 is partially complete only on the left hand side. It is, however, possible to establish the position of the anterior border of the foramen magnum and identify the styloid process, stylomastoid foramen, the lateral extremity of the tympanic plate, the carotid canal, foramen ovale and the infratemporal crest on the left hand side. The position of the petrous apex can be estimated to within a few millimetres of the left hand side. The cranium TM 1517 is partially complete in the region of the cranial base on the left hand side only. The preserved bone allows the position of the anterior border of the foramen magnum to be estimated, and it is possible to locate accurately enough all the landmarks used in this study on the left hand side. The exception is the apex of the petrous temporal bone which, though present, is difficult to define precisely. The Taung skull is in three separate parts; an endocast, the mandible, and the facial skeleton and frontal region of the skull. When the endocast and facial portion are articulated, it is possible to make out the position of the right lateral extremity of the tympanic plate, the carotid canal, petrous apex, foramen ovale and infratemporal crest. Good estimates of the position of the anterior border of the foramen magnum, and of the spheno-occipital synchondrosis can also be made on this specimen.

The partial reconstruction of several of these fossil hominid specimens was considered justified so that, at the very least, good estimates of

comparable measurements could be made on all the fossil specimens. The methods used in the reconstruction are outlined in part ix of the Method section.

TABLE 1

Summary of adult skulls used in this study

	Homo sapiens pooled sexes	Pan troglodytes ♂	Pan troglodytes ♀	Gorilla gorilla ♂	Gorilla gorilla ♀	Pongo pygmaeus ♂	Pongo pygmaeus ♀
The Middlesex Hospital Medical School, Cleveland Street, London	30						
Primate Collection, British Museum (Natural History), London		17	6	11	14	16	9
Powell-Cotton Museum, Birchington, Kent			7	4	1		
Odontological Museum, The Royal College of Surgeons of England, Lincoln's Inn Fields, London						1	4
Sub-Total	30	17	13	15	15	17	13
Total	30	30		30		30	

TABLE 2.

Summary of juvenile skulls (pooled sexes) used in this study

	Homo sapiens	Pan troglodytes	Gorilla gorilla	Pongo pygmaeus
The Middlesex Hospital Medical School, Cleveland Street, London	7			
Primate Collection, British Museum (Natural History), London		32	27	27
Powell-Cotton Museum, Birchington, Kent		36	32	
Odontological Museum, The Royal College of Surgeons of England, Lincoln's Inn Fields, London	19			5
Osteology Department, British Museum (Natural History), Osman Hill Collection	10			
Dental Anatomy Department, University College, London	14			11
Total	50	68	59	43

TABLE 3.

Originals and casts of fossil hominid crania and skulls used in this study

Specimen	Site of origin	Institution where the original fossil is to be found
MLD 37/38	Makapansgat, S.A.	Department of Anatomy, Medical School, University of Witwatersrand, Johannesburg, S.A.
Taung	Taung, S.A.	"
Sts 5	Sterkfontein, S.A.	Transvaal Museum, Pretoria, S.A.
Sts 19	"	"
Sts 25	"	"
SK 47	Swartkrans, S.A.	"
SK 847	"	"
TM 1517	Kromdraai, S.A.	"
OH 5 (cast)	Olduvai Gorge, Tanzania	Original in Museum, Dar-es-Salaam, Tanzania
OH 9 (cast)	"	National Museum of Kenya, Box 40658, Nairobi, Kenya
OH 24	"	"
KNM-ER 406	East Rudolf, Kenya	"
KNM-ER 407	"	"
KNM-ER 732	"	"
KNM-ER 1470	"	"
KNM-ER 1805	"	"
KNM-ER 1813	"	"
KNM-ER 3733	"	"
KNM-ER 3883	"	"

CHAPTER 6.

Methods

i. Apparatus.

ii. Definition of anatomical landmarks and definition of measurements made directly from the specimens.

iii. Test of accuracy of measurement techniques.

iv. Radiographic techniques.

v. Definition of anatomical landmarks and measurements made from radiographs of pongid specimens.

vi. The accuracy of the technique used for correcting measurement magnification.

vii. The problem of asymmetry of the cranial base.

viii. Dissection of comparative pongid wet specimens.

ix. Method for reconstructing the cranial base of certain fossil hominid crania.

x. Method of studying muscle markings on the cranial base of certain fossil hominids.

xi. Statistical and analytical methods.

xii. Summary of the materials and measurements used in each of the four separate studies of the thesis.

i. Apparatus

a) Sliding calipers.

Kanon sliding calipers with both pointed and broad jaws were used for the majority of the measurements. Measurements were recorded to the nearest 0.1 mm but for statistical analysis they were rounded up or down to the nearest mm and then transferred to computer cards.

b) Spreading calipers.

G.P.M. 300 mm steel spreading calipers with pointed tips were used. Measurements were made to the nearest mm, and transferred to computer cards.

c) Perspex craniostat.

Radiographs included in the cross-sectional radiographic study of the comparative pongid material were taken using a perspex craniostat. This was made so that radiographs of each specimen could be taken in three planes at right angles to each other. The craniostat was designed and built by the writer to fulfil the following requirements: 1) the instrument should be radiolucent to allow complete and unobstructed radiographs of the specimens to be made; 2) it should be possible to position any skull in three planes at right angles to each other while film and X-ray source remained in a constant relationship to each other; 3) the craniostat should allow small movements of the skull to be made while the skull is in position so that anatomical landmarks can be aligned with the vertical and horizontal scales built into the craniostat; 4) for safety reasons, it should be suitable for use with the X-ray source positioned vertically above the instrument.

The craniostat consisted of a perspex base plate 350 mm x 350 mm. This was considered large enough to support the largest gorilla skull in any plane without the extremities of the skull overlapping the edges. Four

vertical perspex plates, each 50 mm wide and 150 mm high, were fixed to each edge of the base plate. Each of the four vertical perspex plates was positioned so that slides, constructed to slot on top of the plates and held firmly in position by spring-loaded ball catches, could be used to support horizontal perspex rods that were passed through holes drilled parallel in the slides (see Plate 1). The rods could then be extended along the midline of the base plate to meet at the centre.

In this way, rods from slides and vertical plates on opposite sides of the base plate could be used to support skulls so that the Frankfurt Horizontal lay either parallel with or perpendicular to the base plate. Alternatively, two slides placed on the same vertical plate could be used, together with rods having right-angled ends, to support the skull in norma lateralis, with all the midline landmarks of the skull lying in one plane parallel to the base plate (see Plate 2). Any additional support necessary could be provided from horizontal rods supported from the other vertical plates. Horizontal and vertical lines were scored on the vertical plates and were used to orientate the skull. The base plate was levelled with a spirit level before each set of radiographs was taken.

d) X-ray film.

Singulex RP non-screen medical X-ray film was chosen because it was easy to process automatically and because good reproduction was possible without intensifying screens or cassettes. It was also possible to store exposed film of this type for long periods before developing.

e) X-ray machines.

A Philips industrial X-ray machine was used to take radiographs of all specimens kept in the primate collection of the British Museum (Natural History), London. This machine is housed in the X-ray room of the British Museum (Natural History), London. A portable 'Atomscope' X-ray

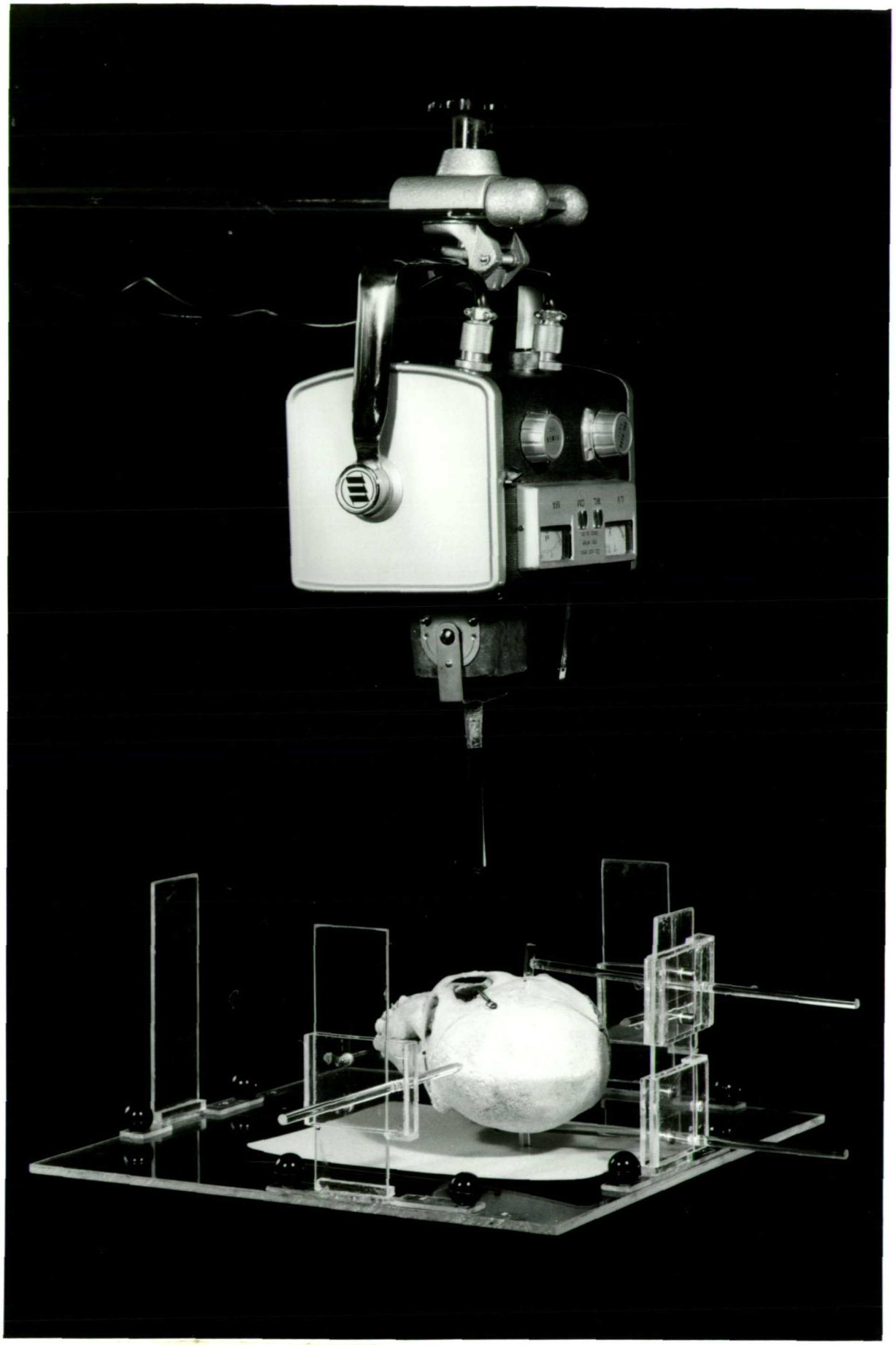


Plate 1. Perspex craniostat and portable 'Atomscope' X-ray machine.

machine (Plate 1) was used to take the radiographs of all the other specimens. This machine was kindly loaned by W.H. Collins, Department of Radiology, The Middlesex Hospital, Mortimer Street, London. Both these machines were capable of high accelerating voltages necessary for good quality radiographs of large dried skulls, and as specimens were completely immobilized, long exposure times could be used.

f) Suitable apparatus for protection was used throughout the radiographic study and included: Lead aprons, film monitor badges developed each month, and lead screens.

ii. Definition of anatomical landmarks

The anatomical landmarks used in the metrical analysis were chosen to provide information about the parts of the ethmoid, sphenoid, temporal and occipital bones, which contribute to the hominoid cranial base. Where possible, they are anatomical landmarks with functional associations, and are also capable of being accurately and precisely defined. Two craniometric points, alveolare and opisthocranion, were chosen to mark the most anterior and posterior limits of the skull in order that the actual length of the cranium could be measured and used to calculate linear magnification on the radiographs of specimens in norma lateralis. The relative position of these landmarks on the cranial base are shown in the diagrams representing individual specimens of Homo sapiens, Gorilla gorilla and Pongo pygmaeus (Figures 5 and 6). When not stated otherwise, the landmarks are defined on the assumption that the cranium is orientated in the Frankfurt Horizontal.

1. AL, alveolare - the lowest point on the process between the alveoli of the upper two central incisors.
2. OPN, opisthocranion - the most posterior point on the skull in the midline.
3. MO - the most medial point on the medial margin of the orbital wall.

4. OC - the most lateral point on the lateral margin of the optic canal.
5. SOF - the most lateral point of the superior orbital fissure.
6. PT, pterion - taken as the most posterior point on the superior border of the greater wing of the sphenoid.
7. HA - the most inferior point on the pterygoid hamulus.
8. NA, nasion - the junction of the frontal and nasal bones in the midline.
9. IT - the most inferior point on the infratemporal crest.
10. FO - the centre of the foramen ovale, taken as the point of intersection of the maximum anteroposterior and mediolateral diameters.
11. SB. sphenobasion - the position, or the estimated position, of the spheno-occipital synchondrosis in the midline.
12. BS, basion - the most inferior point on the anterior margin of the foramen magnum in the midline.
13. OP, opisthion - the point at which the endocranial and exocranial surfaces of the occipital bone meet on the posterior margin of the foramen magnum in the midline.
14. TP - the most inferior point on the lateral extremity of the tympanic plate.
15. PA - the most anterior point on the inferior surface of the petrous temporal bone.
16. CC - the centre of the carotid canal taken as the point of intersection of the maximum anteroposterior and mediolateral diameters.
17. SM - the estimated centre of the stylomastoid foramen.
18. SP - the midpoint of the posterior aspect of the base of the styloid process or the centre of the styloid pit if the process is missing.
19. FM - the lateral margin of the foramen magnum at the point of maximum width.

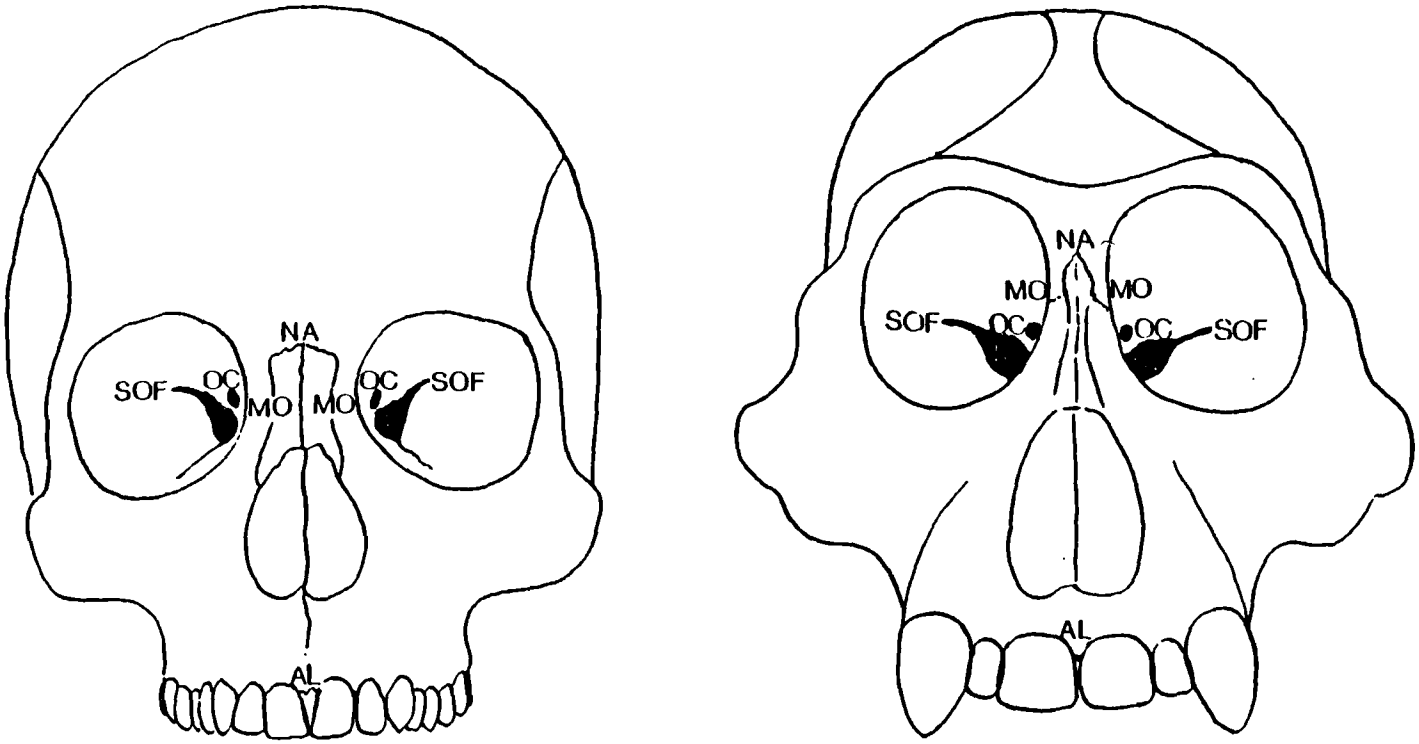


FIGURE 5.

Anatomical landmarks used in this study, seen in norma frontalis, in Homo sapiens and Pongo pygmaeus.

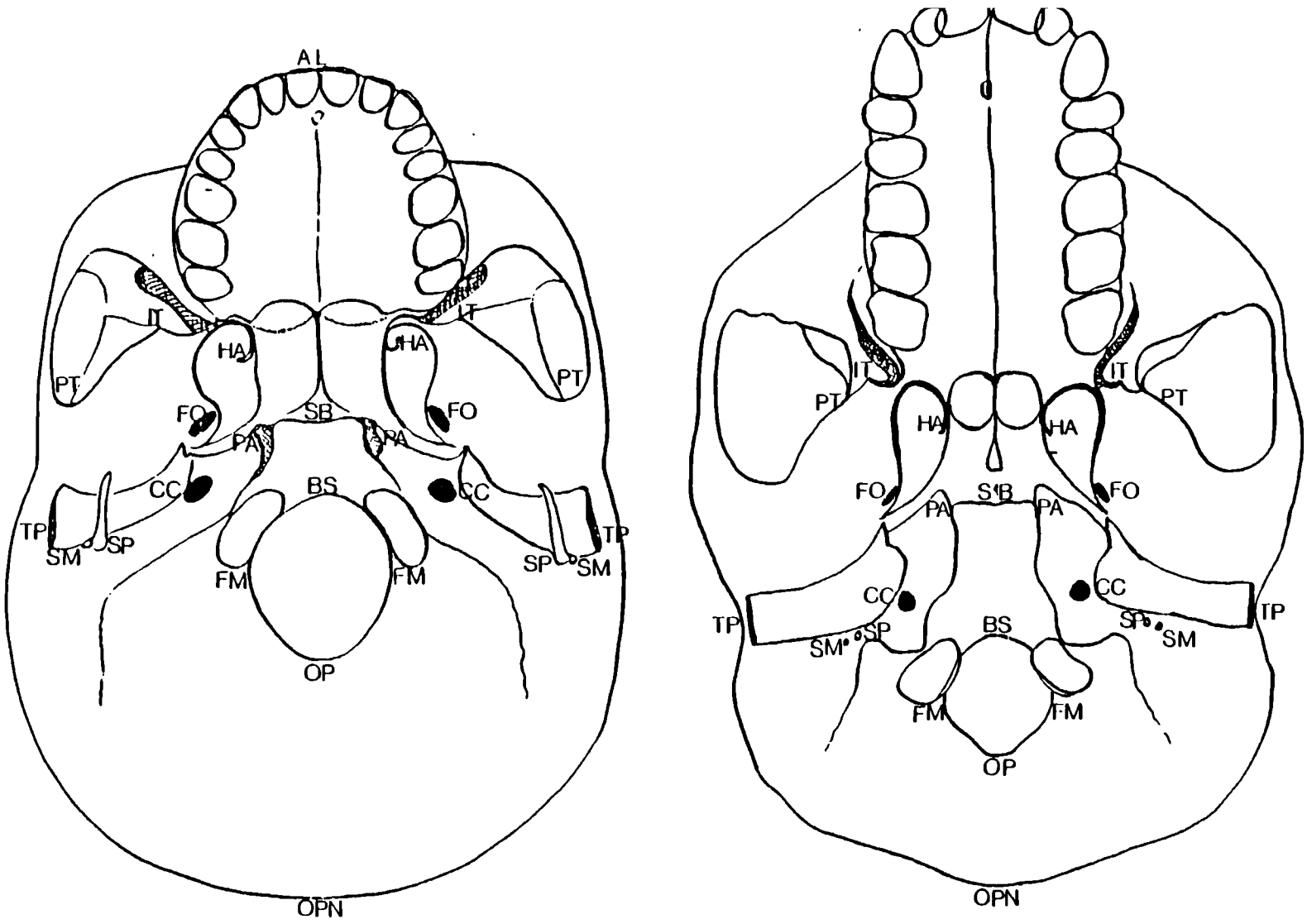


FIGURE 6.

Anatomical landmarks, seen in norma basilaris, in Homo sapiens and Gorilla gorilla.

Definition of linear measurements made directly from the specimens

Each of the following measurements (1-22) were made on all the specimens of Gorilla gorilla, Pan troglodytes and Pongo pygmaeus. Measurements 1, 2, 3, 16, 17, 18 and 19 (used to correct for radiographic magnification and in the growth study) were not made on the specimens of Homo sapiens for reasons explained in section xii of the methods. The measurements were made in the following order.

1. (spreading calipers) Maximum length of skull: (AL - OPN)
2. (spreading calipers) Maximum width of skull: (wherever found)
3. (sliding calipers) Minimum interorbital width: (MO - MO)
4. (sliding calipers) Bi infratemporal fossa width: (IT - IT)
5. (sliding calipers) Bi foramen ovale width: (FO - FO)
6. (sliding calipers) Bi carotid canal width: (CC - CC)
7. (sliding calipers) Bi petrous apex width: (PA - PA)
8. (sliding calipers) Bi tympanic width: (TP - TP)
9. (sliding calipers) Maximum width of foramen magnum: (FM - FM)
10. (sliding calipers) Maximum length of foramen magnum: (BS - OP)
11. (sliding calipers) Bi styloid process (or pit) width: (SP - SP)
12. (sliding calipers) Bi stylomastoid foramen width: (SM - SM)
13. (sliding calipers) Length of the basioccipital: (SB - BS)
14. (sliding calipers) Length from petrous apex to carotid canal: (PA - CC)
15. (sliding calipers) Length from carotid canal to tympanic plate: (CC - TP)
16. (sliding calipers) Bi optic canal width: (OC - OC)
17. (sliding calipers) Bi superior orbital fissure width: (SOF - SOF)
18. (spreading calipers) Bi pterion width: (PT - PT)
19. (sliding calipers) Height of pterygoid plate: (IT - HA)
20. (sliding calipers) Length of basicranium from IT-TP: (IT-IT / TP-TP)
21. (sliding calipers) Length from foramen ovale to tympanic plate: (FO-FO TP-TP)
22. (sliding calipers) Length from infratemporal crest to anterior edge of foramen magnum: (IT-IT / BS)

The angular measurements α (31) and β (32) defined in the section of the methods on radiographic procedures (section v) were also made directly from the specimens of Homo sapiens with a protractor. The comparability of angular measurements made with a protractor, either from radiographs or directly from the specimens, is demonstrated in section vi of the methods, and it was considered unnecessary to take basal radiographs of the Homo sapiens sample (and impossible to take radiographs of the fossil specimens) simply to record these two angular measurements.

iii. Test of accuracy of measurement techniques

Measurements were checked to demonstrate how poor instrument technique and imprecise definition of bony landmarks affected their accuracy and precision. The method adopted by Zuckerman (1955) was followed in this thesis. Ten measurements of widely varying size and type were recorded five times on single specimens of Homo and Pan. For each variable the range of intra-measurement variation was expressed in terms of the variation in the relevant population sample.

TABLE 4. Measurement error, expressed as a percentage of the sample range, for ten measurements repeated five times on specimens of Homo and Pan

	Homo	Pan
Bi PA	2.5	3.3
Bi IT	12.0	1.8
Bi FO	8.8	5.5
Bi CC	3.1	2.0
Bi TP	2.9	7.6
Bi FM	2.5	13.8
CC - TP	13.0	8.0
IT-IT/TP-TP	13.0	14.2
IT-IT/BS	13.0	12.9
BS - OP	4.5	5.0
Mean measurement error	7.5	7.4

The mean percentage average error for the Homo sapiens sample was 7.5% and for the sample of Pan troglodytes 7.4%. The range of error varied from 2.5% to 13% in the Homo sample and from 1.8% to 14.2% in the Pan sample.

High values for percentage error were not associated with small measurements nor low values with large measurements. High values were associated with landmarks that were either difficult to define precisely (IT), or were slightly damaged on the two specimens used for repeated measurements and some measurements (e.g. IT-IT/TP-TP) were simply more difficult to make accurately than others.

The mean percentage measurement errors of 7.4% and 7.5% (i.e. equivalent to 1 mm error in a 15 mm distance) were considered acceptable.

iv. Radiographic techniques

The radiographic study of Gorilla gorilla, Pan troglodytes and Pongo pygmaeus was carried out to provide comparative growth data about endocranial and angular measurements which could otherwise not be made. Much of this information has already been collected in longitudinal growth studies of Homo sapiens, and has been reviewed in Chapter 2. It was considered unnecessary to repeat these observations in this study, and so radiography was confined to the pongid taxa. The study was designed to comply with the following criteria:

1. That exocranial anatomical landmarks used on the specimens could be accurately identified on the radiographs of each specimen.
2. That accurate comparisons of measurements made directly on the specimens themselves could be made with measurements made on radiographs.

To satisfy the first criterion, radio-opaque markers were attached to the skulls where anatomical landmarks were not easily seen on radiographs. One mm lead shot, fixed in position with Bostik clear adhesive, or plasticine mixed with a quantity of finely turned dental silver alloy, were used as

radio-opaque markers. The following anatomical landmarks were marked.

NA - Midline

SB - Midline

PT - Left and right hand sides

OC - Left and right hand sides

SOF - Left and right hand sides

IT - Left and right hand sides

PA - Left and right hand sides

CC - Left and right hand sides

TP - Left and right hand sides

The second criterion was met by (a) reducing the image magnification to a minimum, and (b) by employing a reliable technique to correct for image magnification on each individual specimen.

Magnification and distortion of the image was reduced to a minimum by:

1. Keeping the object plane parallel, and as close to the film, as possible.
2. Ensuring that the focus film distance was as large as practically possible, i.e. 110 cm.
3. Ensuring that the centre of the X-ray source was positioned centrally over the object and film.
4. Using as small a focal spot as possible.

The theory underlying the technique used to correct image magnification

X-rays behave in a manner similar to light and the image or shadow that they cast is magnified proportionally if the conditions to minimise distortion, listed above, are observed.

When the X-ray source is vertically above the object, and when the plane of the object is parallel with the film or image plane, the total magnification of the object is proportional to the magnification of any one part of the object (Figure 7). In the figure the object, 100 mm long, is magnified to 120 mm or 20%. Each 10 mm part of the object is also magnified 20%

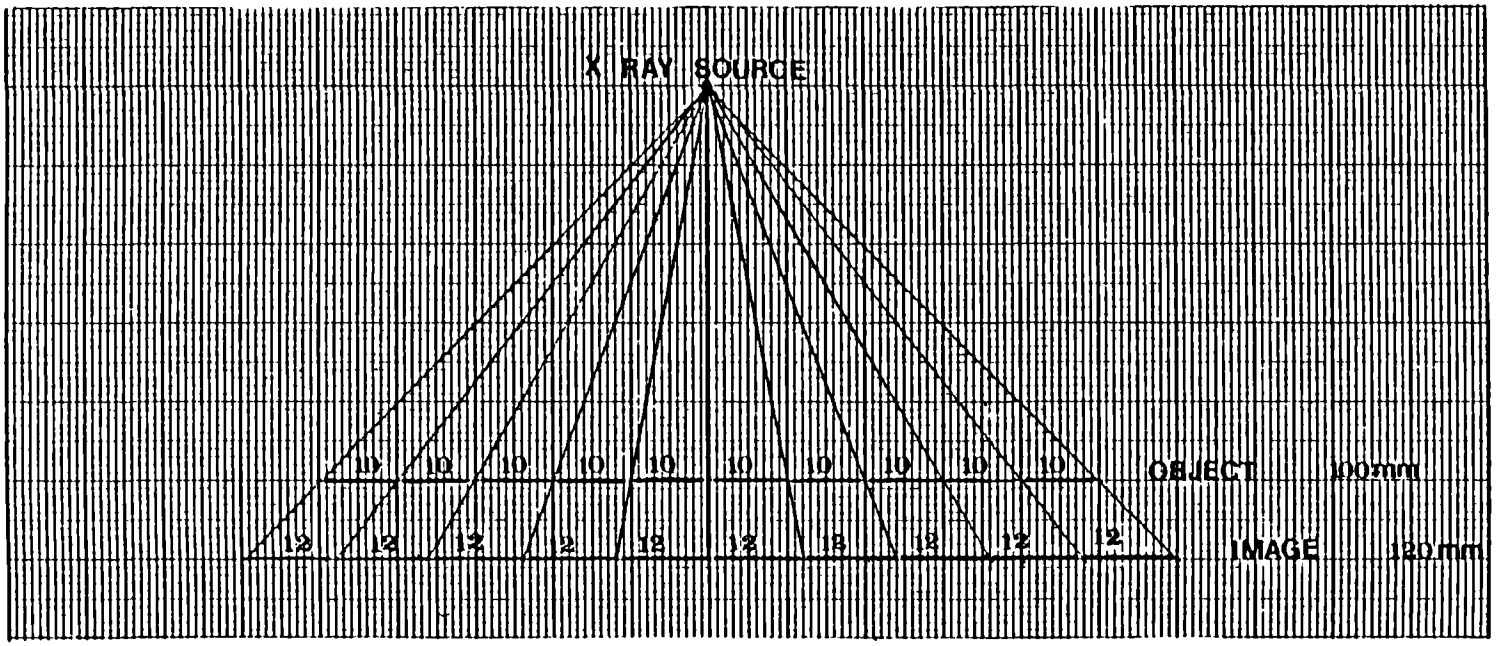


FIGURE 7.

Diagram illustrating the theoretical magnification of an object 100 mm long and 50 mm away from a point X-ray source.

to measure 12 mm long. This means that if the total magnification of skull length, measured from opisthocranion to alveolare is known, then the magnification of any part of the skull lying in the same plane will be the same as this. However, this cannot be applied to parts of the skull lying nearer to or further from the film. Uniform magnification of this sort also means that angular measurements recorded in one plane parallel to the film will not be distorted and no correction for magnification will be necessary. Grøn (1960) has demonstrated that even when small differences in the angulation of the object plane to the central ray occur ($\pm 5^{o}$) there are no measurable changes in the size of projected angular measurements and that linear measurements on cephalometric radiographs only deviate by 0.8% or less from values obtained when the object is parallel to the film. Zuckerman (1955) and Ashton (1957) have also demonstrated that all parts of the cranial base (situated in the same plane) when measured on lateral radiographs of specimens were magnified to the same extent.

In this study, the degree of magnification for each specimen was calculated for the lateral radiographs by comparing the actual known length of the skull (from opisthocranion to alveolare) with the measured length on the radiograph. The degree of magnification of the basal radiographs was calculated in a similar manner by comparing the actual maximum width (wherever found) with the maximum width of the skull measured directly from the radiographs. Radiographs of specimens made in norma frontalis were used only in the determination of relative dental age (see Chapter 7) and no magnification correction was necessary.

Measurements of length and angular measurements made in the sagittal plane were made from the radiographs taken in norma lateralis. Similarly, width and angular measurements made in norma basilaris, were made on the radiographs taken in norma basilaris. In this way it was possible to correct for magnification, and thus reliably predict the actual measurements on each

skull. A test of this technique appears in section vi of the methods.

Before each set of radiographs was taken the craniostat was positioned on a sheet of lead, to prevent any reflection of X-rays back onto the film, and then levelled with a spirit level. Before each individual skull was positioned for the radiograph being taken, the film (in its envelope) was placed on the perspex base plate.

Three radiographs were taken of each individual pongid skull:

1. Norma basilaris. For this radiograph, the skull was positioned in the craniostat with two straight perspex rods fixed from opposite upright supports in the external auditory meati. The lead markers at the lateral extremities of the tympanic plate (TP) and the Frankfurt Horizontal were both positioned so that they were parallel with the base plate (Plate 2A).

2. Norma lateralis. The skull was positioned with two locating rods (each with right angled points fixed from the same upright support) in the left and right external auditory meati. The midsagittal plane was defined by an imaginary line running through the following midline landmarks; alveolare, staphylion, hormion, sphenobasion, basion, opisthion and opisthocranion. This imaginary midline plane was then positioned parallel to the perspex base plate (Plate 2B).

3. Norma frontalis. The skull was positioned with the two straight perspex rods fixed from opposite upright supports, positioned in the external auditory meati with the Frankfurt Horizontal perpendicular to the perspex base plate (Plate 2C).

On no occasion was the position of the skull determined from the external auditory meati; these points were used solely to hold the skull while the position was defined exactly from either midline sagittal landmarks or the Frankfurt Horizontal relative to the perspex base plate upon which the film was placed. For all radiographs, the X-ray source was positioned 110 cm from the plane of the film. Typical exposure times were

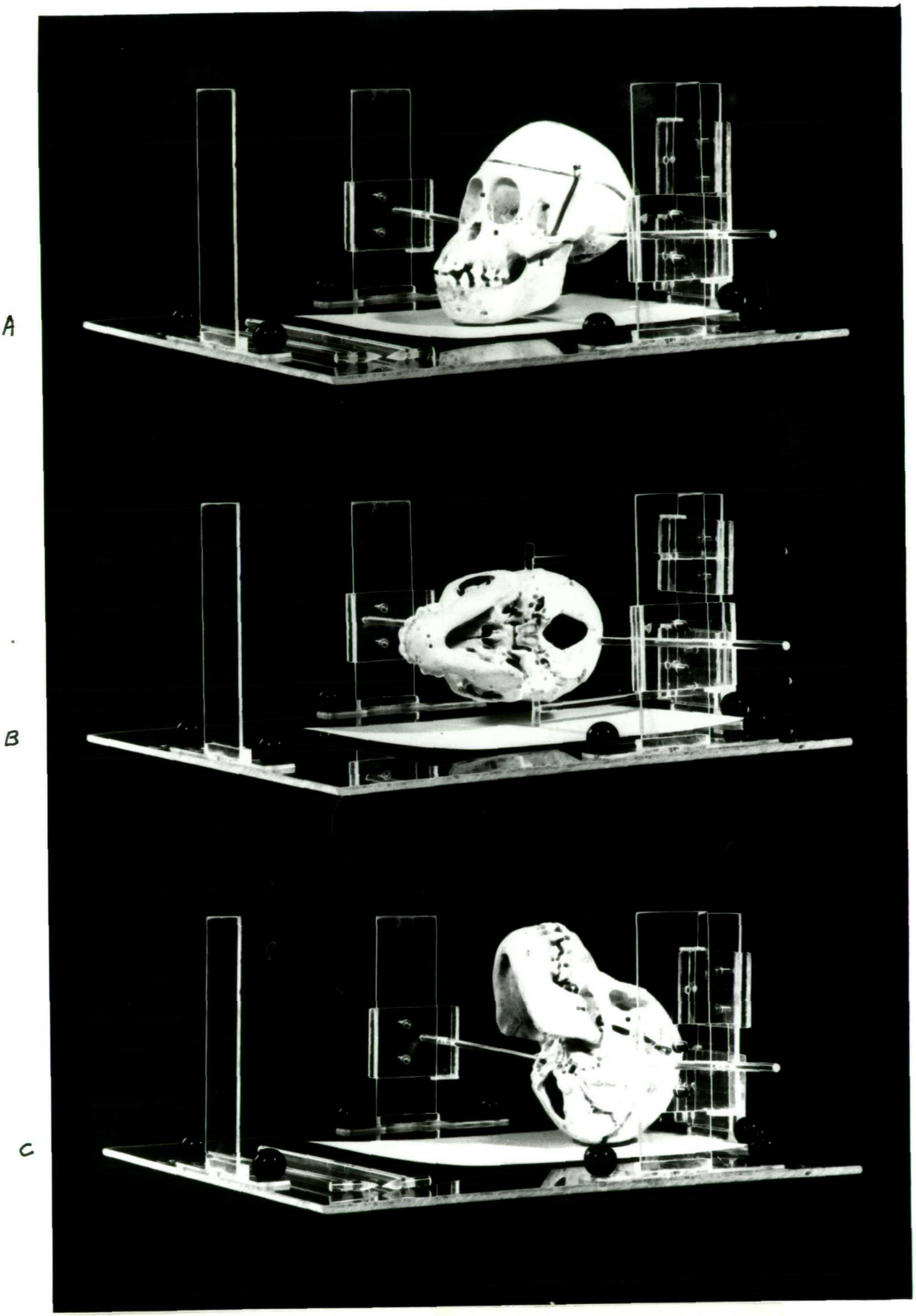


Plate 2. Perspex craniostat with skulls positioned in

A; norma basilaris, B; norma lateralis and
C; norma frontalis.

7 seconds at 6MA and 60KV on the industrial machine, and 4 seconds at 12MA and 68KV on the portable 'Atomscope'. These values were determined by experimentation and were varied slightly for very small or very large skulls. The current and accelerating voltage on the portable machine were fixed, it only being possible to vary the exposure time. A total of 775 radiographs were taken of 170 juvenile and 85 adult pongid dried skulls. All the films were developed, fixed and dried using an automatic developing machine.

v. Definition of anatomical landmarks and measurements made from radiographs of the pongid specimens.

a) Definition of anatomical landmarks used for measurements made on radiographs

The anatomical landmarks defined in the midline and used for measurements made from the lateral radiographs are illustrated for a single specimen of Pan troglodytes in Figure 8. The angular measurements made from the radiographs taken in norma basilaris are shown in Figure 9.

1. AL, alveolare - The lowest point on the process between the alveoli of the upper two central incisor teeth.
2. OPN, opisthocranion - The most posterior point on the skull in the midline.
3. NA, nasion - The intersection of the internasal suture with the fronto-basal suture.
4. FC - The foramen caecum, or most anterior point of the cribriform plate when seen in the lateral or basal plane.
5. CL - The most posterior point on the cribriform plate when seen in the lateral or basal plane.
6. CR - The most lateral point on the lateral margin of the cribriform plate when seen in the basal plane.
7. PS, prosphenion - The most anterior point of the ethmoidal spine of

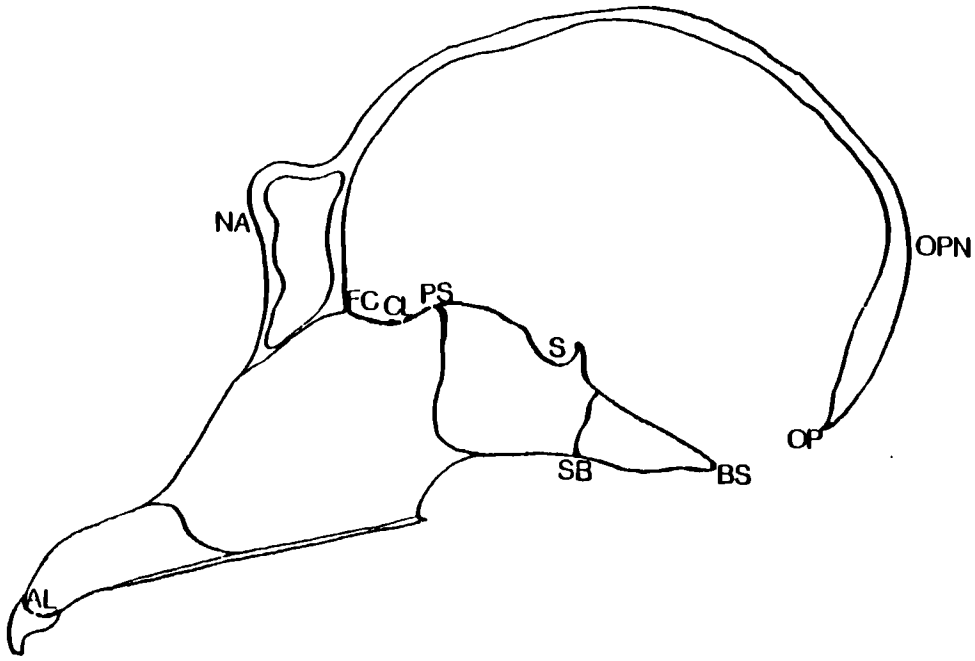


FIGURE 8.

The midsagittal section of a specimen of Pan troglodytes illustrating the midline anatomical landmarks used in the radiographic study.

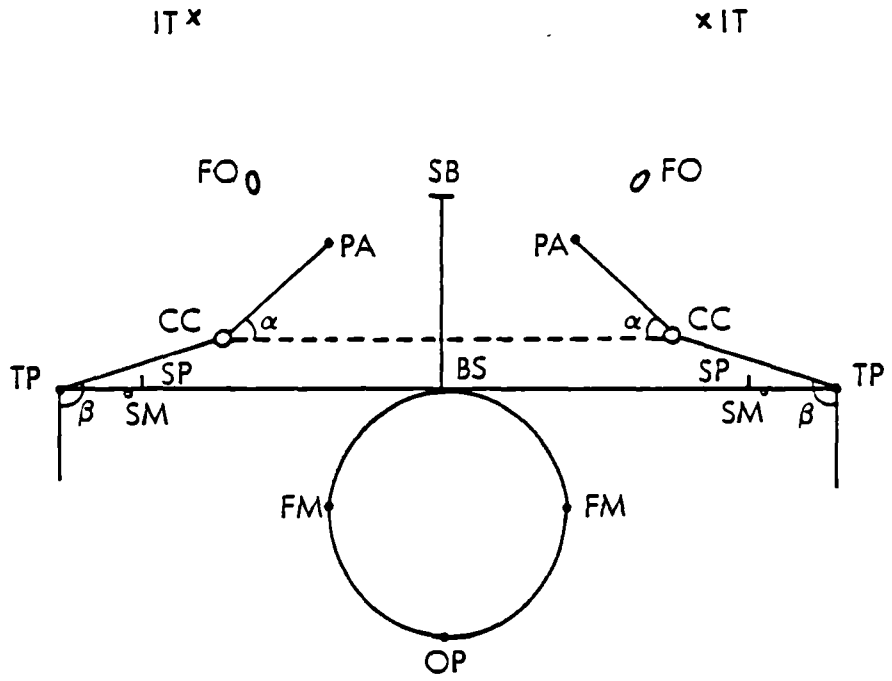


Fig. 9. Skull base diagram of *Homo sapiens* with landmarks and angular measurements. Actual size.

the sphenoid bone, taken as the intersection of the ethmoidal crest on the anterior wall of the sphenoidal sinus with the floor of the anterior cranial fossa.

8. SB, sphenobasion - The estimated position of the spheno-occipital synchondrosis in the midline.
9. S, sella - The midpoint of the sella turcica as determined by inspection.
10. CC - The centre of the carotid canal taken as the point of intersection of the maximum antero-posterior and medio-lateral diameter.
11. TP - The most inferior point of the lateral extremity of the tympanic plates.

b) Definition of measurements made from radiographs of pongid specimens

Measurements made from the lateral radiographs

23. (sliding calipers) Maximum length of the skull: (AL - OPN)
24. (sliding calipers) Length of the frontal bone in the midline: (NA - FC)
25. (sliding calipers) Length of the cribriform plate: (FC - CL)
26. (sliding calipers) Length of the ethmoid bone: (FC - PS)
27. (sliding calipers) Length of the sphenoid bone: (PS - SB)
(Measured as the shortest distance between two lines projected perpendicular to the Frankfurt Horizontal from PS and SB.)
28. (protractor) Cranial base angle γ : (formed by FC - S - SB)

Measurements made from the basal radiographs

29. (sliding calipers) Maximum width of the skull: (wherever found)
30. (sliding calipers) Width of the cribriform plate: (CR - CR)
31. (protractor) Angle α : (Angle between bi carotid canal line joining the centres of the carotid canals and the axis of the petrous temporal bone: CC - CC - PA)
32. (protractor) Angle β : (Angle between the parasagittal plane running

through the lateral end of the tympanic plate (TP), and the line joining TP and the centre of the carotid canal (CC))

vi. The accuracy of the technique for measurement magnification

To test the accuracy of the technique used to correct measurement magnification, two measurements made on 18 of the basal radiographs were corrected by the percentage magnification factor computed from the actual maximum width of the skulls and the apparent maximum width of the skulls on the basal radiographs. These values were then compared with values for the measurements made directly from the skulls. The measurements used were No. 7 (bi petrous apex breadth) and No. 8 (bi tympanic breadth). Both were made on 18 adult specimens of Pan troglodytes and two sets of measurements were recorded to the nearest mm.

TP - TP Actual Measurement from specimen	TP - TP Computed value from X-ray	PA - PA Actual Measurement	PA - PA Computed value from X-ray
98	99	25	24
102	102	24	23
100	99	22	22
101	101	25	23
102	101	23	23
106	104	27	26
112	113	23	22
106	105	23	23
109	107	25	24
100	100	25	24
95	95	25	24
98	98	26	25
99	99	25	24
103	104	27	25
90	91	28	27
109	110	20	20
101	99	28	27
104	104	28	26

Out of the total of 36 comparisons, 11 corrections were 100% correct; 18 differed by 1 mm from the actual measurement; and the remaining 7 differed by 2 mm. This degree of accuracy, ranging from 0% to 8% was considered acceptable, most of the error probably being due to measurement error and not the correction technique.

To test the comparability of angular measurements made from the radiographs (in the case of the three pongid taxa) or directly from the specimens (in the case of the Homo sapiens and fossil specimens), seventeen juvenile Pongo pygmaeus specimens from the primate collection of the British Museum (Natural History), London were chosen at random and measurement 31 (angle α), measured directly from the specimens (α), was compared with the values for the same measurement made from the radiographs (α').

Index No.	α	α'	Actual difference	Percentage difference
032	69	70	1	1.4
1948.831	70	71	1	1.4
1976.14.10	65	68	3	4.6
110	69	70	1	1.4
1976.14.13	68	65	3	4.4
046	65	67	2	3.0
1852.32.12	70	70	0	0
1976.14.41	68	67	1	1.4
3n	77	76	1	1.2
1844.32.07	60	61	1	1.6
32	67	65	2	2.9
3t	58	60	2	3.4
1082	62	63	1	1.6
1.3.74	60	60	0	0
44.3.2.08	60	59	1	1.6
1859.2.10.02	60	61	1	1.6
67.4.12.2	65	62	3	4.6

The mean percentage difference between the two measurements was 2.1%. The range of difference between the two was 0% - 4.6%. This degree of comparability was considered acceptable and comparison of angular measurements recorded from radiographs and directly from the specimens was considered to be justified.

vii. Asymmetry of the cranial base

Five measurements on the cranial base were made on both left and right sides of each specimen. Four of these measurements were used to investigate asymmetry of the cranial base. This was done to justify using the mean right and left hand side values for measurements No. 14, 15, 19, 31 and 32 in the analyses, and to test for any significant asymmetry in the cranial base which might affect bilateral measurements made across the midline. This test was also carried out to provide some justification for the method of reconstruction of certain fossil hominid crania (see section ix). The measurements used to test for asymmetry were:

14. Length from cartoid canal to petrous apex (CC - PA)
15. Length from carotid canal to lateral tympanic extremities (CC - TP)
31. Angle α
32. Angle β

The means and standard deviations for 25 specimens of Homo, Pongo, Gorilla and 24 specimens of Pan were calculated for all the left and right hand measurements of 14, 15, 31 and 32. The values for the left and right hand sides were compared for each taxa and Student's t test was used to assess the significance of these differences.

TABLE 5. Results of measurements made on the left and right hand sides of 99 skulls to test for the degree of asymmetry of the cranial base

	PA - CC		CC - TP		α		β	
	L	R	L	R	L	R	L	R
Homo sapiens								
N = 25								
$\bar{X}$	18.7	19.1	21.6	21.9	106.7	107.4	44.5	46.2
S.D.	2.5	2.6	2.7	2.8	2.74	2.2	5.8	5.3
t	0.554		0.385		0.995		0.108	
P	P = 0.6/NS		P = 0.7/NS		P = 0.4/NS		P = 0.8/NS	
Gorilla gorilla								
N = 25								
$\bar{X}$	30.4	30.6	41.3	40.8	95.48	96.84	73.2	73.0
S.D.	3.5	3.7	3.38	4.1	3.38	3.1	4.32	4.37
t	0.195		0.451		0.148		0.195	
P	P = 0.4/NS		P = 0.7/NS		P = 0.9/NS		P = 0.9/NS	
Pan troglodytes								
N = 24								
$\bar{X}$	23.8	24.0	32.7	31.8	97.0	96.9	69.9	70.3
S.D.	2.38	2.32	2.78	3.12	4.32	4.32	5.88	4.0
t	2.950		1.060		7.850		2.690	
P	P = 0.8/NS		P = 0.2/NS		P = 0.4/NS		P = 0.7/NS	
Pongo pygmaeus								
N = 25								
$\bar{X}$	27.4	27.9	34.6	34.8	100.8	100.6	68.8	69.2
S.D.	5.21	3.25	3.74	3.72	3.88	4.34	2.22	1.95
t	0.407		0.190		0.240		0.609	
P	P = 0.7/NS		P = 0.8/NS		P = 0.8/NS		P = 0.5/NS	

These results demonstrate that in all cases, the values of P suggest that the null hypothesis, that the left and right hand sides of samples of crania have the same mean values, should not be rejected.

The results also suggest that there is no significant asymmetry between left and right hand sides of the skull base when viewed in norma basilaris. In the light of this finding, it seems justifiable to reconstruct the fragmentary fossil crania by the methods outlined in section ix of the methods, and to use the mean values recorded on the left and right hand sides of the specimens in the results section.

viii. Dissection of wet comparative pongid specimens

Complete dissections of the head and neck of the adult male specimens of Pongo pygmaeus and Pan troglodytes were made. The major stages of the dissection were photographed and detailed notes made throughout the dissection. Where possible, the less complete specimens of Gorilla gorilla and Pan troglodytes were dissected to display the cranial attachments of muscles in the region of the skull base. Photographs, notes and measurements were then made of all these dissections.

Descriptions of the dissections were then compiled detailing the relationships of muscles associated with the cranial base. These are presented with photographs of the dissections.

ix. The method of reconstructing the cranial base of certain fossil hominids

In order that measurements identical with those made on the adult comparative material could be made on each of the damaged fossil specimens, an imaginary midline was constructed running through any two, or more, midline structures in the sagittal plane. The landmarks of the damaged side were then projected as a mirror image of the preserved side. This procedure was considered justifiable in the light of the findings in section vii. Any two or more of the following landmarks were used to construct

the midline; prosthion, staphylion, hormion, sphenobasion, basion, opisthion or opisthocranion.

In this way, estimates of certain bilateral measurements on the following damaged specimens were derived by doubling the value of the distance from the undamaged side to the midline: Sts 25, Sts 18, MLD 37/38, SK 847, TM 1517, Taung, KNM-ER 732, KNM-ER 1470, KNM-ER 1813, KNM-ER 1805, OH 24 and OH 9 (cast). These estimated measurements appear in Table 10 of the results in brackets.

The cranial base is particularly poorly preserved in KNM-ER 1470; nonetheless, by using the preserved margins of both foramina ovale and the right carotid canal, and part of the right petrous temporal bone, it is possible to estimate the distances FO - FO, CC - CC and the angle α. The positions of the infratemporal crest (preserved on the right hand side) and the lateral extremities of the tympanic plate can also be estimated.

Measurement technique is invariably very difficult when working with fossil remains and great care is essential when identifying anatomical landmarks. Where there was any difficulty or doubt about measurements made from the fossil sample, they also appear in brackets in Table 9 of the results.

All measurements on the fossil specimens were made using either sliding calipers or a protractor, and were recorded to the nearest mm or degree.

x. The method of studying muscle markings on the cranial base of certain fossil hominids

Notes, measurements and drawings of the basicranial muscle markings were made from the original specimens of MLD 37/38, Sts 5, SK 47, OH 24, KNM-ER 406, KNM-ER 407, KNM-ER 1805 and KNM-ER 1813. The outlines of the most probable cranial attachments of muscles in these fossils were carefully painted on to duplicate plaster casts of these fossil hominids.

The painted casts were then orientated in norma basilaris and photographed. The photographs and descriptions of the muscle markings appear in the results section, Chapter 11.

xi. Statistical and analytical methods

Sample statistics

The mean value, range and standard deviation for each variable of the samples of adult comparative taxa were first calculated by hand with a calculator and then checked by computer programme when individual measurements had been transferred to computer cards.

The coefficient of variation was computed by hand for each variable in the adult groups, using a calculator and the formula:

$$C.V. = \frac{100\ S}{\bar{X}}$$

the significance of the difference between the measurements made on the left and right hand sides of the cranial base (Section) was computed using the formula:

$$t = \frac{(\bar{X}_1 - \bar{X}_2) \sqrt{\frac{N_1 N_2}{N_1 + N_2}}}{\sqrt{\frac{(N_1 - 1) S_1^2 + (N_2 - 1) S_2^2}{N_1 + N_2 - 2}}}$$

The quantity t was then compared with the cumulative student's t distribution table, using $N_1 + N_2 - 2$ degrees of freedom, given in Simpson, Roe and Lewontin (1960). There was no reason to assume that any individual measurement would vary undiscretionally, so the 'two-sided' hypothesis was used to test the level of significance of the t values.

The application of more complicated and advanced analytical techniques are not included in this thesis for reasons set out at the end of the discussion.

xii. Summary of the materials and measurements used in each of the four parts of the thesis study.

1. Metrical study of the adult hominoid cranial base

Thirty adult specimens of each of the four comparative taxa were used to establish a metrical framework which could be used to examine the significance of any differences in the size and shape of the cranial base of fossil hominids. The samples of Gorilla gorilla, Pan troglodytes and Pongo pygmaeus were sexed so that as far as possible equal numbers of males and females (see Table 1) were present in each taxa. The sample of adult Homo sapiens skulls were not sexed.

The following measurements were used in this study:
Nos. 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 20, 21, 22, 31 and 32. The angular measurements 31 and 32 were made directly from the specimens of the Homo sapiens sample and from the radiographs in each of the three pongid samples.

2. Study of growth changes occurring in the hominoid cranial base

This study was designed to supplement the adult metrical study and to provide additional information about ontogenetic changes occurring in the cranial base of Homo sapiens, Gorilla gorilla, Pan troglodytes and Pongo pygmaeus. Good data about growth changes in the ethmoid and sphenoid bones (especially in the sagittal plane) in Homo sapiens are available and have already been reviewed in Chapter 2. Information about ontogenetic changes in the ethmoid and sphenoid bones of Gorilla gorilla, Pan troglodytes and Pongo pygmaeus is much more limited.

Each of the seventeen measurements made on the four comparative taxa in the adult study (in norma basilaris) were also made in the same way on the juvenile specimens of Homo sapiens, Gorilla gorilla, Pan troglodytes and Pongo pygmaeus. However, additional measurements were made to provide comparative data about growth in the regions of the ethmoid and

sphenoid bones in Gorilla gorilla, Pan troglodytes and Pongo pygmaeus. The additional measurements were:

Nos. 3, 16, 17, 18, 19, 24, 25, 26, 27, 28 and 30.

They were made on 30 adult and 59 juvenile specimens of Gorilla gorilla, 30 adult and 67 juvenile specimens of Pan troglodytes, and 25 adult and 42 juvenile specimens of Pongo pygmaeus.

3. Dissection study of the muscles of the cranial base region in Gorilla gorilla, Pan troglodytes and Pongo pygmaeus

Two specimens of Gorilla gorilla, two specimens of Pan troglodytes and one specimen of Pongo pygmaeus were dissected for this study and are described in Chapter 5.

4. Metrical analysis of the cranial base of fossil hominids

The measurements used in this study were identical to those used in the adult metrical study, i.e. Nos. 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 20, 21, 22, 31 and 32.

CHAPTER 7.

The method of ageing individual skulls

Individual specimens of Gorilla gorilla, Pan troglodytes and Pongo pygmaeus were judged to be adult if the lateral skull radiographs of each specimen showed complete formation and closure of the root apices of the permanent canines and third molars. Specimens of Homo sapiens were judged to be adult if the third upper and lower molars were completely erupted and in occlusion.

The problem of ageing juvenile crania

Introduction

Most comparative cross-sectional growth studies have used the state of eruption of the developing dentition to divide subadult specimens into developmental subsets, or stages. However, whereas the developmental events underlying the timing and sequence of gingival eruption in the human dentition are well documented, there is no such data base for the apes, and it is thus difficult to apply a reliable time scale to these events in pongids.

A system often used for assessing the age of human individuals is the 'atlas' method, and this has been applied to radiographs of the developing dentition taken between birth and maturity (Schour and Massler, 1940). Generally, this is an effective and practical way of ageing skulls which are to be used in cross-sectional growth studies.

Radiographs of all the juvenile pongid material used in this growth study were made in three planes at right angles to each other, as described in the section on radiographic methods (Chapter 6, Section iv). Given the availability of the radiographs, it seemed reasonable to devise a system for ageing juvenile pongid crania from the radiographic appearance of their developing dentitions. The details of this study, and of the relevant

literature concerned with odontogenesis in man and the three great apes, are presented elsewhere (Dean and Wood, 1981b) but a brief summary of the study is presented here.

Materials, and methods used, for the study of pongid dental development

A total of 175 juvenile ape skulls from the Primate collections of the British Museum (Natural History), London and the Powell-Cotton Museum, Birchington, Kent were used in this study of pongid dental development.

Radiographs were taken of 60 Gorilla gorilla, 75 Pan troglodytes and 40 Pongo pygmaeus skulls. All the skulls were of immature individuals, ranging in 'age' from infants, with incomplete deciduous dentitions, to juveniles with incompletely formed roots of the permanent canine and third molars. The number of specimens used in this study is greater than that used in the growth study due to the fact that some were included in the former but rejected from the latter because of damage to the cranial base region. The sex of some individuals is known from museum records, but it was impossible to determine the sex of the remaining sample, even on the basis of the developing permanent canine teeth. The numbers of males and females is therefore unknown. In addition to the three extra-oral views already described, 30 intra-oral periapical radiographs were taken to clarify ambiguities observed on the larger films.

In addition to these radiographic data, ground sections of all the permanent mandibular teeth of single specimens of Pan, Gorilla and Pongo were prepared to provide histological evidence of incremental growth markings in the various dental tissues.

The three radiographs of each juvenile ape skull show all the developing teeth in the upper and lower jaws. Teeth begin to develop at different times during the growth period, so in any one skull there are teeth at early stages of development and others at more advanced stages. Tooth formation is a continuous process and there is no clear cut division, or

quiescent period, between any of the developmental stages. The radiographic definitions of the dental developmental stages used in this study are shown in Figure 10 and are those which, with minor modifications, have been used in most radiographic studies of the developing human dentition. They are inevitably arbitrary stages of development. For example, the angulation of the incremental growth lines in the dentine of a tooth is such that root formation must begin before crown formation is complete (see Dean and Wood, 1981b).

No differences between the developmental stages of mandibular and maxillary teeth could be detected in this study. As mandibular teeth are more easily seen on radiographs, they were used in preference to maxillary teeth, but in cases where mandibular teeth were missing, their maxillary counterparts were substituted. No account was taken of the state of eruption of any of the teeth in the jaw. Skulls in which all the teeth were at developmental stages intermediate to those shown in Figure 10 were excluded from this part of the study. All skulls in which two or more teeth in the same jaw coincided with any of the stages A-K defined in Figure 10 are given in Table 6. Thus Table 6 provides a basic plan for the developmental stages of all the mandibular teeth. No asymmetry between left and right sides was noted.

A 'time scale' for these coinciding developmental events was devised as follows. Longitudinal human studies indicate that formation of the mandibular first, second and third molar crowns takes approximately the same time (Moorrees et al, 1963; Gleiser and Hunt, 1955). There are no such data for the pongid dentitions but it has been assumed, for the purpose of this study, that first, second and third molar crown formation in the three pongid taxa also takes the same time. This has been estimated at 2.5 years, because there is no histological evidence to indicate that M_1 crown formation begins before birth, and because gingival eruption occurs between 3.25 and 3.5 years with a quarter of the root already completed

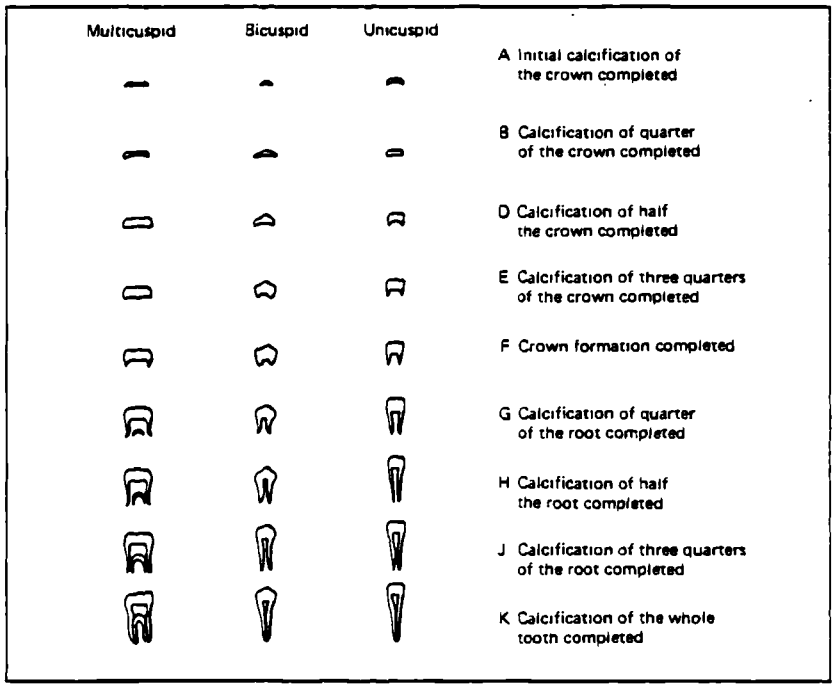


Fig.10. Radiographic appearance of the developmental stages A–K as they have been defined for unicuspid, bicuspid, and multicuspid teeth. Images are viewed in the buccolingual plane.

Table 6. Table showing the numbers of individuals in *Gorilla*, *Pan* and *Pongo*, in which the developmental stages A–K are coincident

Tooth	Stage	Tooth	Stage	Tooth	Stage	Tooth	Stage	Tooth	Stage	Tooth	Stage	Tooth	Stage	Numbers of individuals with tooth stage combination		
														Gorilla	*Pan*	*Pongo*
dm_1	F	di_1	F	di_2	F	I_1	A	I_1	A					1	–	2
$d\bar{c}$	F	M_1	B											1	–	–
di_1	K	di_2	K	I_1	B	I_2	B	$\bar{C}$	A					4	3	–
dm_1	K	I_1	D	I_2	D	M_1	E							1	1	–
$d\bar{c}$	K	I_1	E	I_2	E	P_3	A	P_4	A	M_1	F	M_2	A	5	2	3
I_1	F	I_2	F	P_3	D									4	2	1
I_1	H	I_2	H	P_3	F	P_4	F	M_3	A	M_2	F			6	3	5
$\bar{C}$	F	M_1	K	M_3	B									2	5	3
I_1	K	I_2	K	P_3	H	P_4	H	M_3	E					3	5	1
P_3	J	P_4	J	M_2	J	M_3	F							3	4	4
P_3	K	P_4	K	M_2	K	M_3	G							4	3	1
C	K	M_3	K											–	–	1

(see Dean and Wood, 1981b). It has also been assumed that the roots of similar teeth (e.g. all molars or all incisors) take approximately the same time to form.

Results

The coinciding developmental stages, A-K, of the deciduous and permanent teeth of Gorilla, Pan and Pongo are shown in Table 6. The three pongid taxa have been represented in one generalised diagram because comparison of the radiographs showed that there were no significant differences in the pattern of dental development of Gorilla, Pan and Pongo. By assuming that molar crown formation takes 2.5 years, that M_1 crown formation begins at birth, and that the roots of similar teeth take the same time to form, the observations in Table 6 were used to construct Figure 11. Data for the mean gingival eruption times of pongid teeth have been incorporated into Figure 11 so that the proportion of root formed on the pongid teeth at the time of gingival eruption could be estimated. Longitudinal data for the human mandibular dentition have been included in the diagram for comparison.

The data in Figure 11 have been used to prepare a reference chart of the developing pongid dentition (Figure 12). Using the principles of the 'atlas' method, this chart can be used to give a relative dental age to radiographs of immature pongid skulls.

To test the use of the chart as an ageing method, measurements were made on a series of Gorilla skulls, made up of 50 juveniles and 22 adults. The distance from alveolare to the lingula of the mandible was measured on each of the specimens and used to represent jaw length. Length of the jaw was then plotted against the relative dental age of each specimen, computed using the dental reference chart (Figure 13). In this figure, the event s in dental development which are usually used to divide juvenile skulls into sub-groups are marked above the horizontal scale.

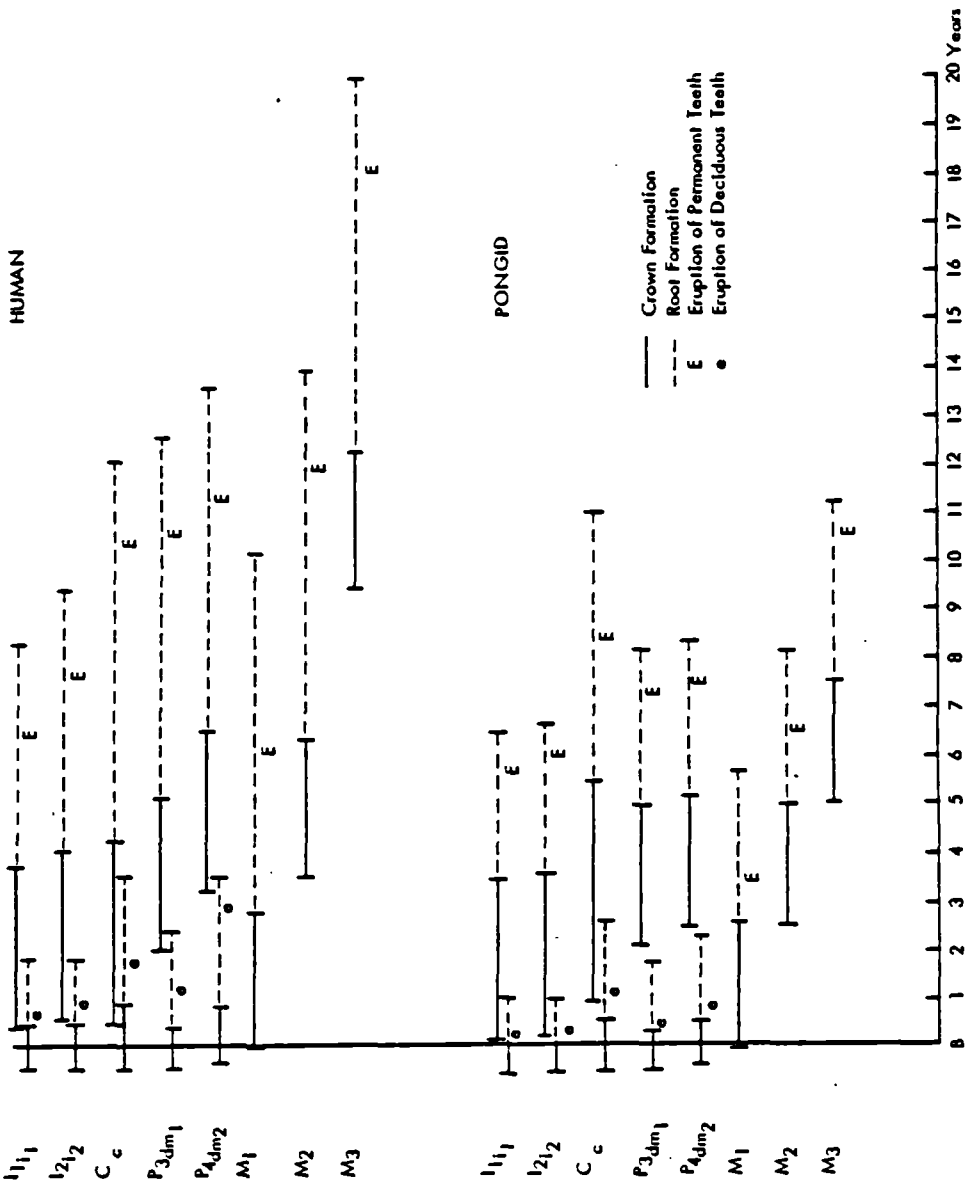
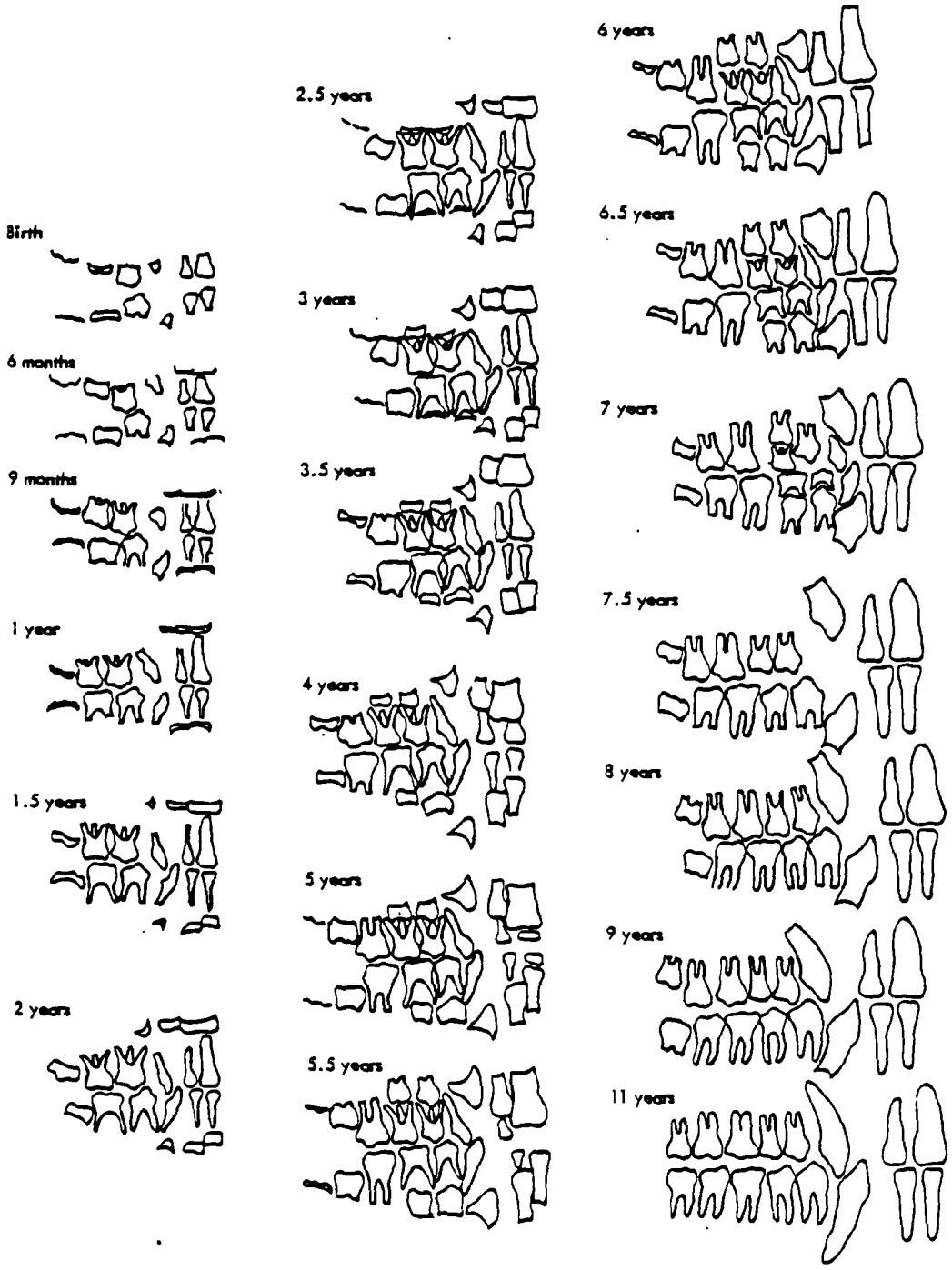


Figure 11
Calcification Times in Years for the Developing Human and Pongid Dentitions

Figure —

Chart of the Developing Pongid Dentition



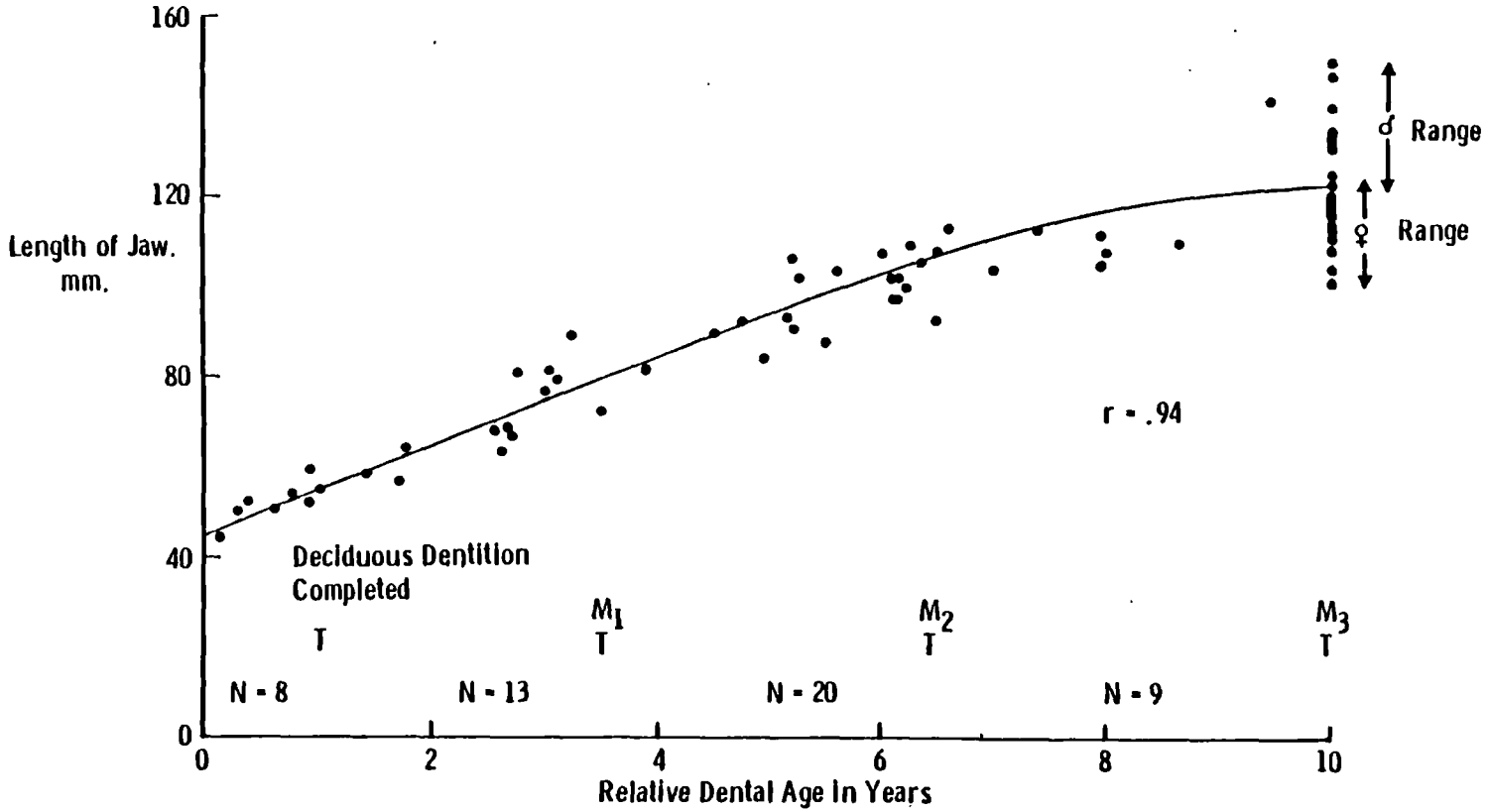


FIGURE 13.

Length of the jaw plotted against relative dental age for juvenile and adult Gorilla crania. Time of complete eruption of the deciduous dentition, and the times of the eruption of M_1, M_2 and M_3 are indicated. Numbers of juvenile individuals within each of the subgroups demarcated by these events are shown at the base of the figure.

The plot shown in Figure 13 shows that there is a significant correlation between relative dental age and jaw length, and when the data are displayed in this way, it is clear that the juvenile gorilla skulls form a continuous series. This finding highlights an inherent defect in studies which group subadult pongid crania into subsets based on gross criteria of tooth eruption. Inevitably, these subdivisions are broad ones and include differing proportions of the total growth period. A more precise estimate of dental ageing greatly enhances the sensitivity of investigations which use subadult pongid material. Another feature of the plot is the gradual increase in variance which, though seldom documented, is often a feature of growth processes.

It is important to realise that cross-sectional data of any kind cannot reveal individual differences in the rate of growth, nor can they establish the timing of particular events within the growth period. Without longitudinal data it is impossible to establish the variability of dental development with chronological age; only the relative dental developmental age of an ape skull can be established from cross-sectional data such as these.

It would be wrong to place too much confidence in data based on cross-sectional material. However, until comprehensive longitudinal data are available, the framework presented in this study is offered as an alternative for ageing pongid crania.

Method used to age individual juvenile skulls and to check the accuracy of radiographic and metrical data.

Each individual juvenile specimen of Gorilla gorilla, Pan troglodytes and Pongo pygmaeus was given a relative dental age by comparison of the radiographs of each specimen with the chart of pongid dental development (Figure 12). The juvenile Homo sapiens sample was given a relative dental age by direct observation of the developing dentitions (many of which were dissected to reveal developing teeth) and comparison with the dental

development chart devised by Schour and Massler (1940). A scale of 0 - 40 units was used, each unit representing six months. All 32 measurements made on the pongid sample were then tabulated, specimen by specimen, in order of increasing relative dental age. Bivariate plots were then made by hand of each series of measurements for each taxon to demonstrate the general features of the growth curves. Any specimen that did not appear to fit in with the general trend was singled out and both the assessment of relative dental age, and the measurements concerned, were checked against the radiographs and/or the original specimen. In this way inaccuracies were revealed before the data were transferred to computer cards.

PART III RESULTS.

Chapter 8. Results of the adult metrical study.

Chapter 9. Results of the study of postnatal growth changes in the cranial base of hominoids.

Chapter 10. Results of the dissection study of the cranial base region in Gorilla gorilla, Pan troglodytes and Pongo pygmaeus.

Chapter 11. Results of the metrical study of fossil hominid crania and of the study of muscle markings on the cranial base of certain fossil hominids.

CHAPTER 8.

Results of the adult metrical study

The mean $\bar{X}$, standard deviation (s.d.), coefficient of variation (CV) and observed range of each of the 22 measurements made directly on the adult specimens in the extant comparative sample, and of the 10 measurements made from the radiographs, are presented in Table 7.

The results of the 17 measurements made on the cranial base seen in norma basilaris are also presented in the form of two-dimensional plots. These are presented for each taxon and use the mean values of the linear and angular measurements to show the relative position of these landmarks on the basicranium (Figure 14).

The results of the remaining measurements made on the three pongid taxa are made use of in the section on growth of the skull base.

Commentary on the cranial base diagrams

An important feature of the results is the similarity of the pattern of cranial base measurements in the three pongid taxa. The cranial base in all three taxa is elongated, with the bilateral landmarks lying close to the midline, and with the petrous axes pointing forwards. The tympanic plates are also elongated, and the tympanic axes lie almost horizontally across the skull base. The foramen magnum is positioned well behind the bitympanic line and the body of the sphenoid bone is long and relatively narrow, when measured across the infratemporal fossa.

In the modern human cranial base pattern, the infratemporal fossa, foramen ovale, petrous apices, carotid canals, styloid processes and stylomastoid foramen all lie relatively further away from the midline than they do in the pongids. In contrast, the lateral extremities of the tympanic plates in Homo sapiens lie much closer together, due to a considerable reduction in their length. The petrous axes in the Homo sapiens sample

Measurement number		1 AL-OPN	2 MAX-W	3 MO-MO	4 IT-IT	5 FO-FO	6 CC-CC	7 PA-PA	8 TP-TP	9 FM-FM	10 BS-OP
Homo sapiens	s.d.				4.5	2.8	3.3	3.3	3.6	2.0	2.7
	$\bar{x}$				65.9	49.6	56.9	32.2	99.3	29.8	35.4
	C.V.				6.8	5.6	5.7	10.2	3.6	6.7	7.6
	Range				57-77	45-56	51-63	27-39	92-108	25-34	29-40
Pan troglodytes	s.d.	10.1	7.6	2.4	3.3	2.7	2.7	2.4	6.5	1.9	2.8
	$\bar{x}$	190.0	124.2	20.2	51.0	43.0	42.6	24.1	104.7	23.4	28.3
	C.V.	5.3	6.1	11.8	6.5	6.2	6.3	9.9	6.2	8.1	9.8
	Range	165-208	109-140	13-26	42-59	37-48	38-48	20-28	90-118	20-28	22-34
Gorilla gorilla	s.d.	28.0	12.7	3.9	4.1	3.3	4.5	2.8	9.4	2.2	2.5
	$\bar{x}$	251.0	152.0	24.6	59.1	51.4	47.4	30.3	131.5	28.6	31.9
	C.V.	11.3	8.3	15.8	6.9	6.2	9.4	9.2	7.1	7.6	7.8
	Range	210-310	131.177	17-33	51-67	42-57	40-57	24-36	116-159	24-33	28.37
Pongo pygmaeus	s.d.	15.9	16.5	3.2	4.7	3.5	4.2	3.4	11.1	2.1	3.0
	$\bar{x}$	210.0	150.9	13.3	51.8	45.1	49.8	29.1	117.5	24.5	30.8
	C.V.	7.5	10.9	24.0	9.0	7.7	8.4	11.6	9.4	8.5	9.7
	Range	179-242	126-174	7-20	46-63	39-54	41-60	21-37	101-137	21-31	24-35

TABLE 7 Parameters and measurements of adult comparative groups.

(i) All linear measurements in millimetres and angles in degrees.

(ii) Measurements 1,2,3,16,17,18,19,24,25,26,27,28 and 39 were not made on the sample of Homo sapiens.

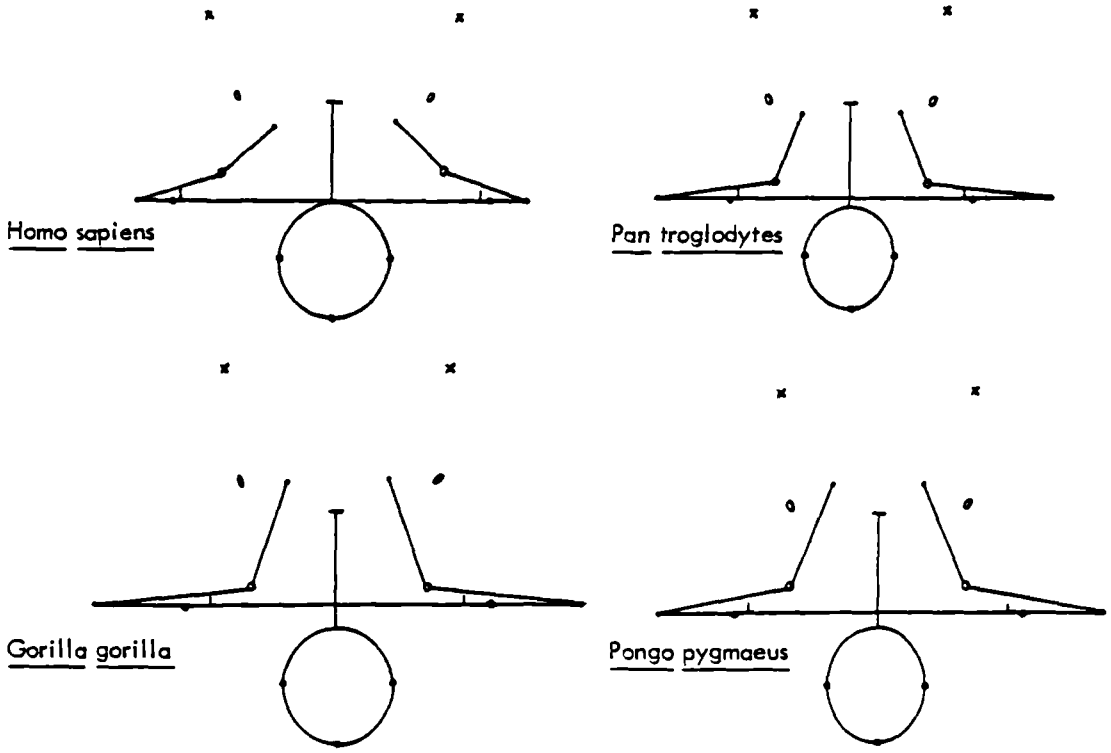
Measurement number		11 SP-SP	12 SM-SM	13 SB-BS	14 CC-PA	15 TP-CC	16 OC-OC	17 SOF-SOF	18 PT-PT	19 HA-IT	20 IT-IT/ TP-TP
Homo sapiens	s.d.	3.9	4.2	2.8	2.3	2.7					3.9
	$\bar{x}$	77.9	81.7	25.6	18.5	21.6					47.9
	C.V.	5.0	5.1	10.9	12.4	12.5					8.1
	Range	72-87	73-91	20-31	14-23	15-26					41-55
Pan troglodytes	s.d.	3.7	3.5	2.4	2.2	2.8	2.3	3.9	3.5	2.7	4.1
	$\bar{x}$	59.6	63.6	26.4	24.1	31.8	25.5	37.2	68.2	27.1	48.8
	C.V.	6.2	5.5	9.0	9.1	8.8	9.0	10.4	5.1	9.9	8.4
	Range	52-66	58-69	20-31	20-29	26-36	21-31	30-44	60-75	21-32	42-56
Gorilla gorilla	s.d.	3.6	4.9	3.0	3.2	3.5	3.1	3.3	4.2	4.6	6.4
	$\bar{x}$	65.8	79.7	31.6	29.8	40.2	31.3	37.6	70.1	33.8	61.2
	C.V.	5.4	6.1	9.4	10.7	8.7	9.9	8.7	5.9	13.6	10.4
	Range	60-72	72-89	25-36	20-37	34-46	25-38	28-44	61-78	27-45	52-75
Pongo pygmaeus	s.d.	5.2	5.2	3.8	3.0	3.8	3.1	3.8	5.9	3.4	6.6
	$\bar{x}$	68.1	76.0	29.9	28.2	34.5	22.4	39.5	68.4	26.1	57.7
	C.V.	7.6	6.8	12.7	10.6	11.0	13.8	9.6	8.6	13.0	11.4
	Range	55-77	65-86	21-38	23-35	27-41	12-26	32-46	57-79	20-34	44-70

TABLE 7, Contd.

Measurement number		21 FO-FO/ TP-TP	22 IT-IT/ BS	24 NA-FC	25 FC-CL	26 FC-PS	27 PS-SB	28 ɣ	30 CR-CR	31 ∝	32 β
Homo sapiens	s.d.	2.5	3.5							5.7	3.3
	x̄	25.9	46.8							45.7	107.1
	C.V.	9.6	7.4							12.4	3.1
	Range	22-32	40-53							31-55	102-113
Pan troglodytes	s.d.	3.1	3.8	3.0	1.2	3.4	2.3	5.4	1.3	5.2	4.8
	x̄	25.0	51.8	19.0	14.4	24.6	22.1	156.1	7.3	68.9	95.8
	C.V.	12.4	7.4	15.7	8.3	13.8	10.4	3.4	17.8	7.5	5.0
	Range	19-32	41-58	13-26	12-17	16-33	17-27	143-168	6-11	55-78	86-105
Gorilla gorilla	s.d.	3.7	7.9	3.5	1.5	2.3	3.8	4.7	1.3	4.7	3.1
	x̄	31.5	68.8	25.6	13.7	19.4	31.7	156.4	9.2	72.0	95.2
	C.V.	11.7	11.4	13.6	10.9	11.8	11.9	3.0	14.1	6.5	3.2
	Range	25-38	52-85	18-34	11-17	16-25	24-41	149-166	7-15	60-81	88-102
Pongo pygmaeus	s.d.	3.6	7.2	2.9	1.5	1.5	3.6	4.0	1.2	3.0	4.0
	x̄	27.8	61.7	21.2	11.5	11.5	36.1	149.5	8.9	68.1	101.0
	C.V.	12.9	11.6	13.6	13.0	13.0	9.9	2.6	13.4	4.4	3.9
	Range	21-38	45-75	12-26	8-15	8-15	29-43	140-158	7-11	60-75	93-109

TABLE 7, Contd.

FIGURE 14.



Cranial base diagrams of Pan troglodytes, Gorilla gorilla, Pongo pygmaeus and Homo sapiens. In all these groups the landmarks are drawn to correspond to their mean value. All diagrams are drawn to the same scale and reduced to 40% of life size.

are rotated in towards the midline, and the ranges of the angle of petrous angulation for Homo sapiens do not overlap any of the pongid taxa. However, it is noteworthy that the coefficient of variation for this angle in Homo sapiens is roughly twice that of the pongid taxa, where it appears to be one of the least variable features of the skull base.

The tympanic axes in Homo sapiens are rotated forwards and are nearly aligned with the petrous axes, but though the mean values for the pongid taxa differ from the mean value for Homo sapiens, the ranges do overlap and the orientation of the tympanic axis is not such a useful discriminating feature as the direction of the petrous axis. The foramen magnum in Homo sapiens is positioned relatively further forward than it is in the pongid taxa.

The mean length of the skull base from the bi-infratemporal crest line to the bi-tympanic plate line is absolutely greater in all three pongids than it is in Homo sapiens, but that part of the skull base roughly equivalent to the length of the body of the sphenoid bone (IT-IT to FO-FO) is markedly foreshortened in Homo sapiens. Thus, the short skull base in Homo sapiens appears to be due to the combination of a more forward position of the foramen magnum, together with a reduction in the length of the body of the sphenoid bone.

Summary of results of adult metrical study

The cranial base patterns of the pongid and modern human skulls are quite distinct. The wider, shorter, cranial base in Homo sapiens contrasts with the longer, narrower, cranial base of the three pongid taxa, the only exception being the bi-tympanic width of the pongid taxa. The orientation of the petrous axis is particularly distinctive, being more horizontal across the skull base in Homo sapiens, whereas in the pongid taxa it lies closer to the sagittal plane.

CHAPTER 9.

Results of the study of postnatal growth changes in the cranial base of hominoids

The results of this study are presented in five sections which summarize the growth of the cranial base in Gorilla, Pan, Pongo and Homo. The first section deals with measurements which reflect the maximum length and width of the cranium and also with overall measurements taken across several bones in the cranial base. The second section presents the data summarizing growth changes in the ethmoid and frontal bones. The third, fourth and fifth sections respectively, present data for growth changes occurring in the sphenoid, temporal and occipital bones of the cranial base. All the measurements presented are plotted against relative dental age. The units of relative dental age correspond to six-monthly periods, from birth to eleven years in the pongid taxa, (0 - 22 units) and from birth to twenty years in Homo sapiens (0 - 40 units). The data used in this chapter are summarized in Table 8. All linear measurements are in mm and angular measurements in degrees.

Measurement number		1 AL-OPN	2 MAX.W.	20 IT-IT/ TP-TP	24 NA-FC	3 MO-MO	25 FC-CL	26 FC-PS	30 CR-CR	4 IT-IT	5 FO-FO
Homo sapiens	Adult $\bar{X}$			48						66	50
	Infant $\bar{X}$			26						45	35
	$\bar{X}$ Growth			22						21	15
	$\bar{X}$ Rate/year			1.0						1.0	0.7
Pan troglodytes	Adult $\bar{X}$	190	124	49	19	20	14	25	7	51	43
	Infant $\bar{X}$	120	87	26	9	9	16	19	6	39	32
	$\bar{X}$ Growth	70	37	23	10	11	NIL	6	1	12	11
	$\bar{X}$ Rate/year	6.3	3.3	2.0	0.9	1.0	NIL	0.5	0.1	1.1	1.0
Pongo pygmaeus	Adult $\bar{X}$	210	152	58	21	13	12	12	9	52	45
	Infant $\bar{X}$	119	90	27	10	7	14	14	8	42	32
	$\bar{X}$ Growth	91	62	31	11	6	NIL	NIL	1	10	13
	$\bar{X}$ Rate/year	8.2	5.6	2.8	1.0	0.5	NIL	NIL	0.1	0.9	1.1
Gorilla gorilla	Adult $\bar{X}$	251	151	61	26	25	14	19	9	59	51
	Infant $\bar{X}$	134	91	28	9	9	16	20	7	42	35
	$\bar{X}$ Growth	117	60	33	17	16	NIL	NIL	2	17	16
	$\bar{X}$ Rate/year	10.6	5.4	3.0	1.5	1.4	NIL	NIL	0.1	1.5	1.4

TABLE 8 Parameters and data of comparative groups presented in growth study.

(i) All linear measurements in millimetres and angles in degrees.
(ii) Measurements 1,2,3,16,17,18,19,24,25,26,27,28 and 30 were not made on the sample of Homo sapiens
(iii) Adult mean values are taken from Table 7. Infant mean values are calculated from individual specimens aged between birth and one year (R.D.A. units, 0-2.0).
(iv) The total mean growth for the whole growth period is calculated as Adult $\bar{X}$ - Infant $\bar{X}$.
(v) The mean rate of growth per year is calculated as the total mean growth divided by 20 years for Homo or 11 years for the three pongid taxa.

Measurement number		16 OC-OC	17 SOF-SOF	18 PT-PT	19 HA-IT	27 PS-SB	28 ♂	6 CC-CC	7 PA-PA	8 TP-TP	11 SP-SP
Homo sapiens	Adult $\bar{X}$							57	32	99	78
	Infant $\bar{X}$							35	17	50	48
	$\bar{X}$ Growth							22	15	49	30
	$\bar{X}$ Rate/year							1.0	0.7	2.4	1.5
Pan troglodytes	Adult $\bar{X}$	26	37	68	27	22	156	43	24	105	60
	Infant $\bar{X}$	16	28	58	13	22	145	30	12	54	47
	$\bar{X}$ Growth	10	9	10	14	NIL	11	13	12	51	13
	$\bar{X}$ Rate/year	0.9	0.8	0.9	1.2	NIL	1.0	1.1	1.0	4.6	1.1
Pongo pygmaeus	Adult $\bar{X}$	22	40	68	26	36	150	50	29	118	68
	Infant $\bar{X}$	13	31	65	13	18	135	33	16	68	47
	$\bar{X}$ Growth	9	9	3	13	18	15	17	13	50	21
	$\bar{X}$ Rate/year	0.8	0.8	0.2	1.1	1.6	1.3	1.5	1.1	4.5	1.9
Gorilla gorilla	Adult $\bar{X}$	31	38	70	34	32	156	47	30	132	66
	Infant $\bar{X}$	16	27	57	12	16	152	32	15	62	48
	$\bar{X}$ Growth	15	11	13	22	16	4	15	15	70	18
	$\bar{X}$ Rate/year	1.3	1.0	1.1	2.0	1.4	0.3	1.3	1.3	6.3	1.6

TABLE 8, Contd.

Measurement number		12 SM-SM	14 CC-PA	15 TP-CC	31 ∝	32 β	9 FM-FM	10 BS-OP	13 SB-BS
Homo sapiens	Adult $\bar{X}$	82	19	22	46	107	30	35	26
	Infant $\bar{X}$	52	14	9	46	102	19	23	15
	$\bar{X}$ Growth	30	5	13	NIL	5	11	12	11
	$\bar{X}$ Rate/year	1.5	0.2	0.3	NIL	0.2	0.4	0.6	0.4
Pan troglodytes	Adult $\bar{X}$	64	24	32	69	96	23	28	26
	Infant $\bar{X}$	49	18	12	58	84	20	26	14
	$\bar{X}$ Growth	15	6	20	11	12	3	2	12
	$\bar{X}$ Rate/year	1.3	0.5	1.8	1.0	1.1	0.2	0.1	1.1
Pongo pygmaeus	Adult $\bar{X}$	76	28	35	68	101	25	31	30
	Infant $\bar{X}$	55	18	19	59	94	22	23	14
	$\bar{X}$ Growth	21	10	16	9	7	3	8	16
	$\bar{X}$ Rate/year	1.9	0.9	1.4	0.8	0.6	0.2	0.7	1.4
Gorilla gorilla	Adult $\bar{X}$	80	30	40	72	95	29	32	32
	Infant $\bar{X}$	55	19	15	62	78	23	29	15
	$\bar{X}$ Growth	25	21	25	10	17	6	3	17
	$\bar{X}$ Rate/year	2.2	1.9	2.2	0.9	1.5	0.5	0.2	1.5

TABLE 8, Contd.

SECTION ONE

Growth changes in the overall dimensions of the cranium

Measurement No. 1: Maximum length of the skull - AL - OPN, Figure 15

Pan, Pongo and Gorilla

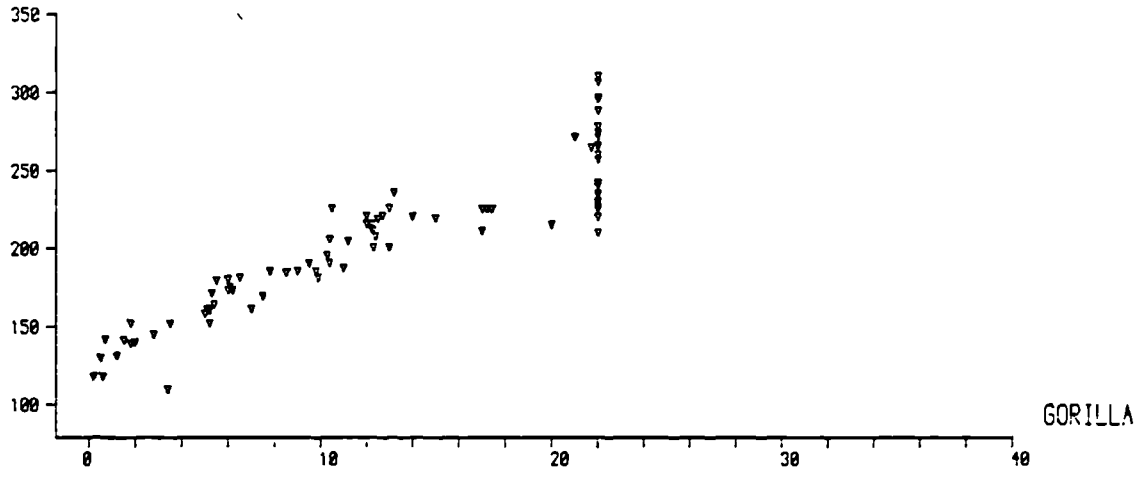
The mean values for this measurement during the first postnatal year in Pan, Pongo and Gorilla are 120, 119 and 134 respectively. In all three taxa, length of the skull increases in a very regular manner throughout the growth period and values within the adult range appear at about $5\frac{1}{2}$ years in all three taxa. The mean adult values are respectively 190, 210 and 251, the greater increases in size in Pongo and Gorilla being due to proportionately greater rates of growth during the whole of the postnatal growth period. This gradual increase in the slope of the graphs for Pan, Pongo and Gorilla is easily seen in Figure 15.

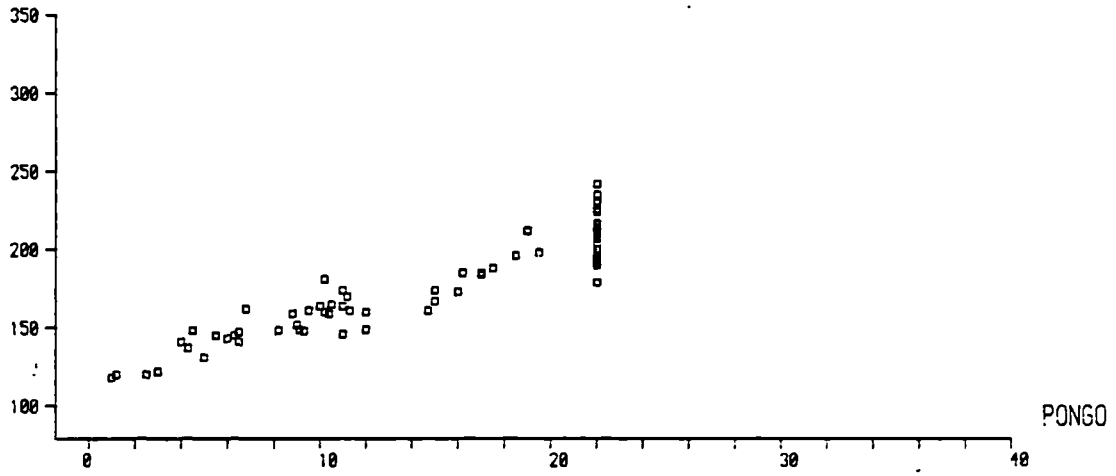
Measurement No. 2: Maximum width of the skull, Figure 16

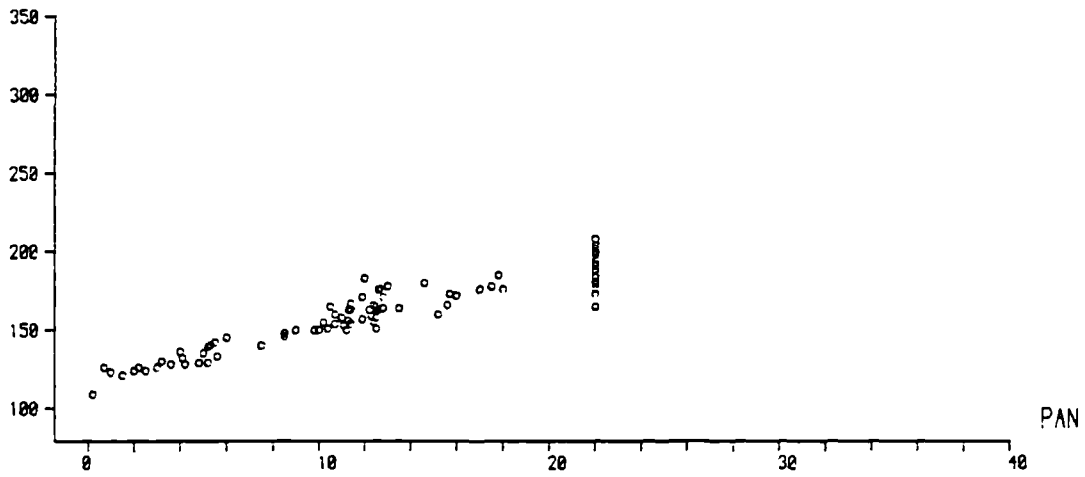
Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 87, 90 and 91 respectively. In Pan and Gorilla, growth is regular throughout the postnatal growth period and values within the adult range appear at $5\frac{1}{2}$ years. The growth curve in Pongo, however, is characterized by a marked increase in the growth rate occurring between 8 years (when values within the adult range first appear) and adulthood. As a result of this, the mean adult values for Pongo and Gorilla are similar, 151 and 152 respectively. The mean adult value for Pan, of 124, is lower than that for Pongo and Gorilla despite the fact that the mean value for Pan during the first postnatal year is similar to that for the other two taxa. This simply reflects the slower rate of growth during the whole of the growth period in Pan.

Figure 15 · AL - OPN







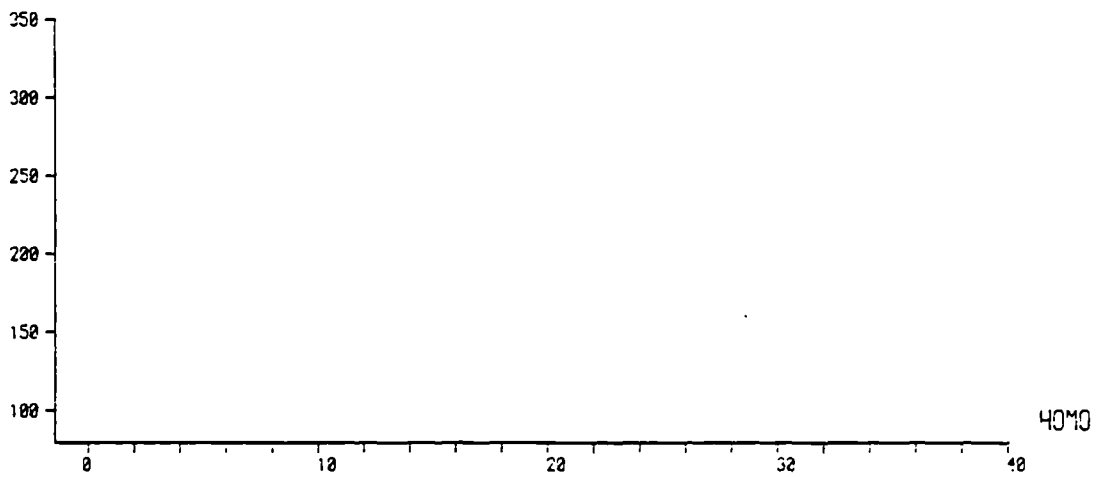
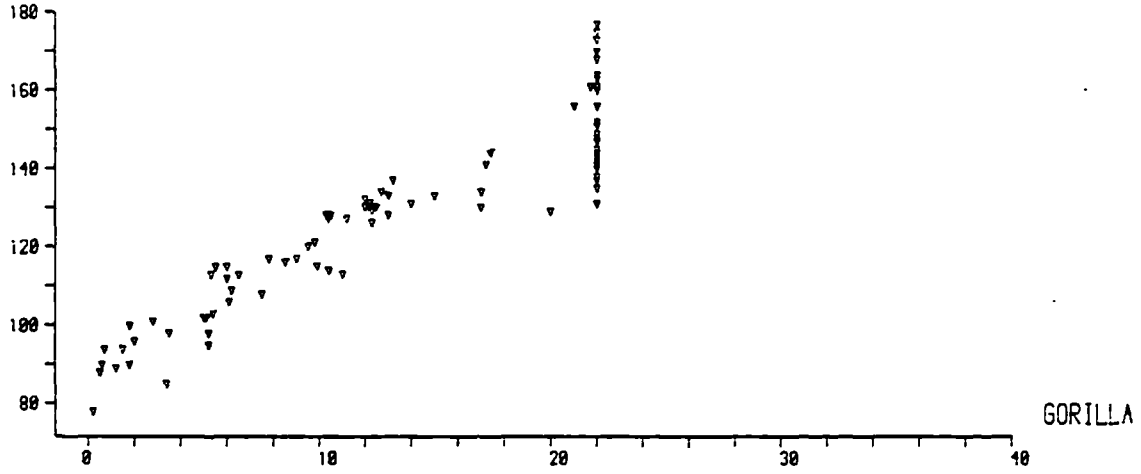
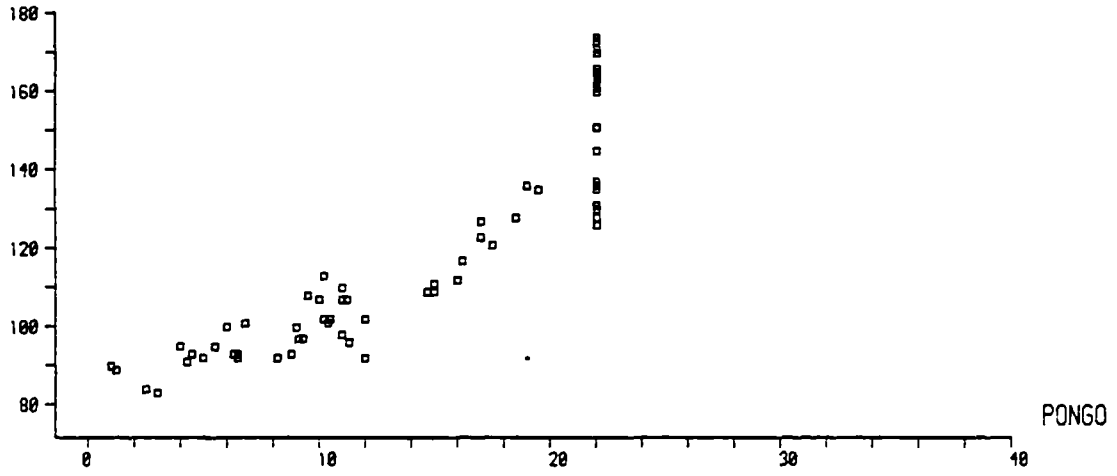
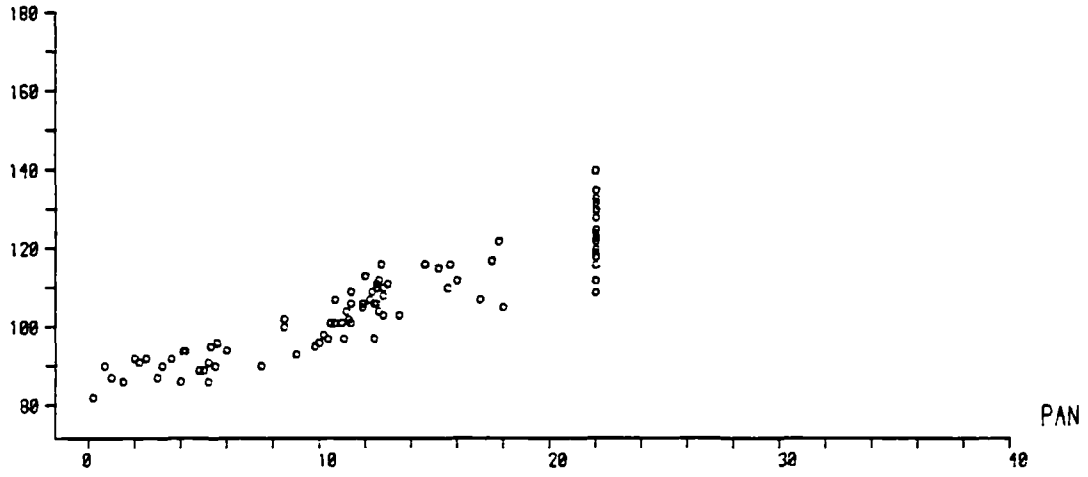
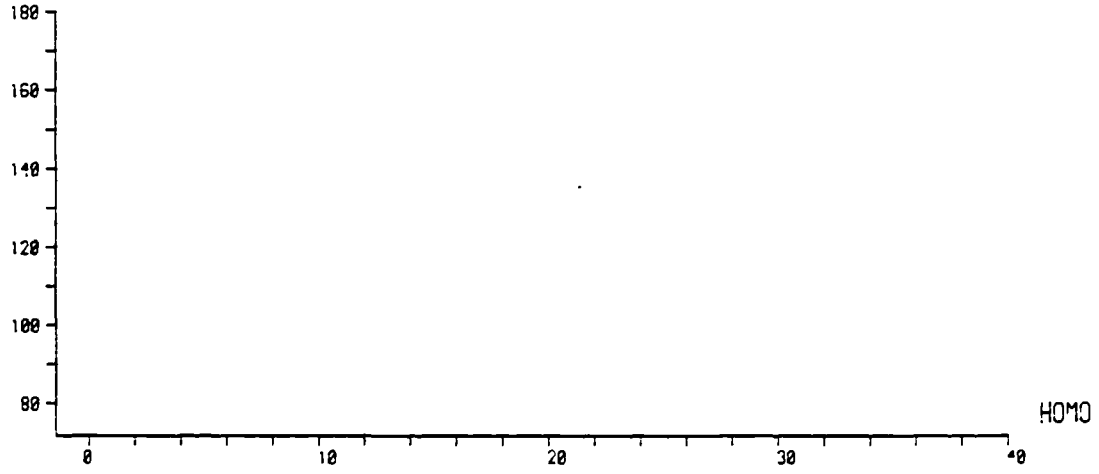


Figure 16 MAXIMUM WIDTH









Measurement No. 20: Overall length of the cranial base - IT-IT/TP-TP, Figure 17

Pan, Pongo and Gorilla

The mean values for the first postnatal year are similar in Pan, Pongo and Gorilla, being 26, 27 and 28 respectively. The mean adult lengths differ slightly, being 49, 58 and 61 respectively, but values within the adult range appear around $5\frac{1}{2}$ years in all three taxa and growth continues to occur until adulthood.

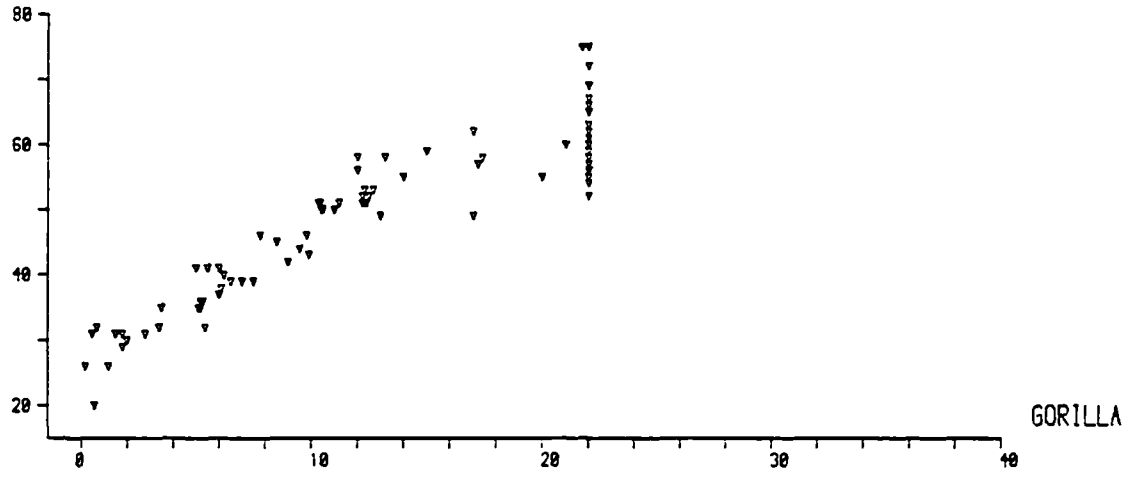
Homo

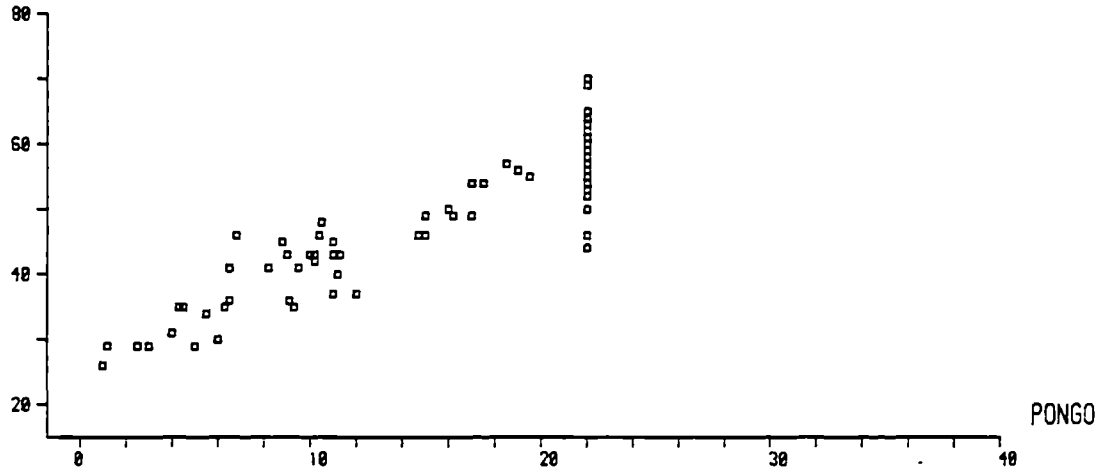
During the first year there is a marked increase in length from 20 to 32. Values within the adult range appear earlier than in the pongid taxa, at about 3 years, after which time there is a slow increase in length to an adult mean value of 48. Little growth occurs after 8 years.

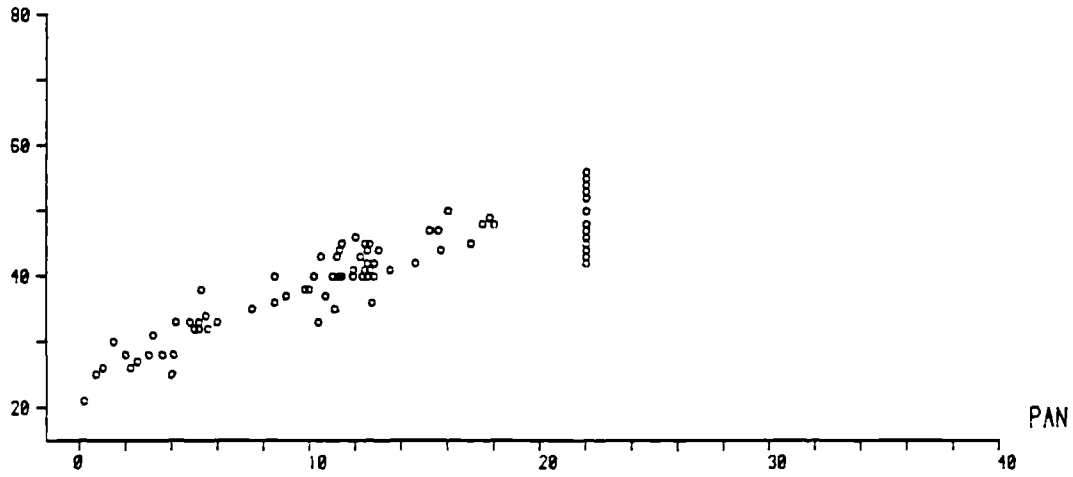
Summary of growth in overall dimensions of the cranium

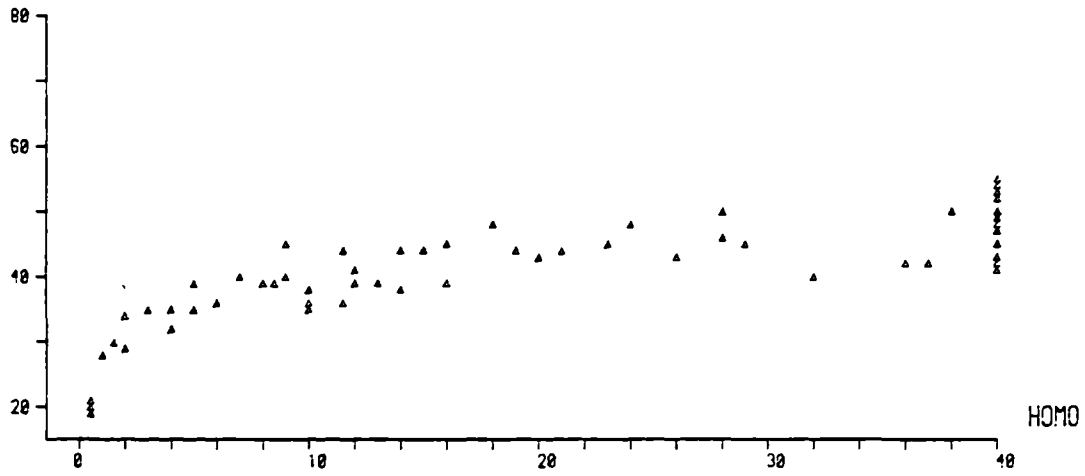
The measurements of maximum length and maximum width of the cranium were made in order that the degree of magnification of the image on the radiographs could be calculated for the pongid taxa. The plots of these measurements are, however, shown here to illustrate the merits of presenting cross-sectional data in this way. It can be seen that the juvenile crania form part of a continuous series and that differences in growth rate can be observed both between taxa and within taxa. The measurement of overall length of the cranial base (Measurement No. 20) shows that important differences between the growth curves of the pongid taxa and that of Homo can be demonstrated by presenting the data in this way. The overall length of the cranial base in Homo sapiens fails to reach the length of the pongid cranial base, despite the marked spurt during the first postnatal year and prolonged growth period unique to Homo sapiens. The average growth rate for this measurement can be calculated by taking the difference between the mean

Figure 17. IT-IT/TP-TP









value for the first postnatal year and the mean value for the adult range and dividing it by the total number of years in the growth period. Calculated in this way, the rate in pongids, about 2.5 mm/year, is more than double that in Homo sapiens (about 1 mm/year on average throughout the whole growth period).

SECTION TWO

Growth changes in the ethmoid and frontal bones

Measurement No. 21: Length of the frontal bone from nasion to the foramen caecum - NA - FC, Figure 18.

Pan, Pongo and Gorilla

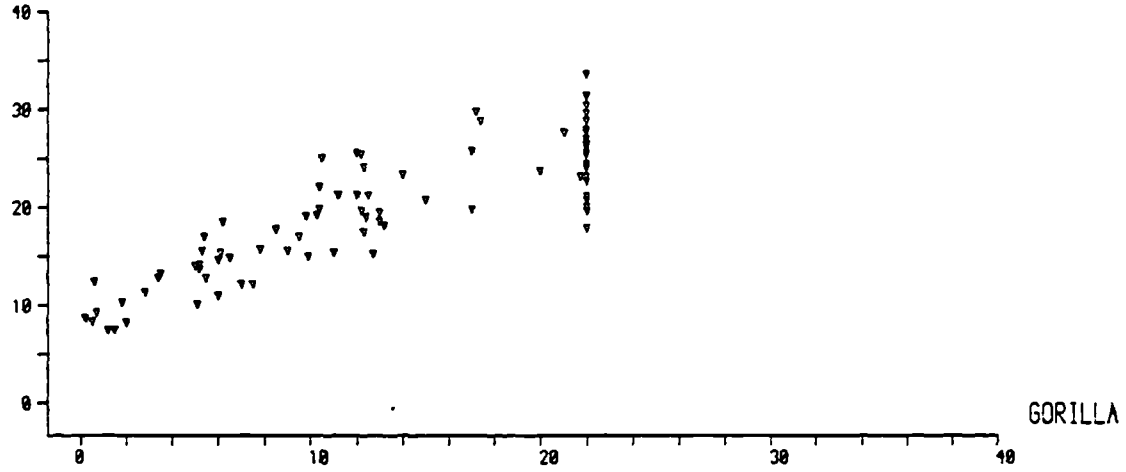
The mean values of 9 and 10 respectively for the first postnatal year in Pan and Pongo gradually increase throughout the growth period to adult mean values of 20 and 21 respectively. The adult mean value of 26 in Gorilla is almost three times the infant mean of 9, whereas in Pan and Pongo the adult mean value is nearer twice the infant mean.

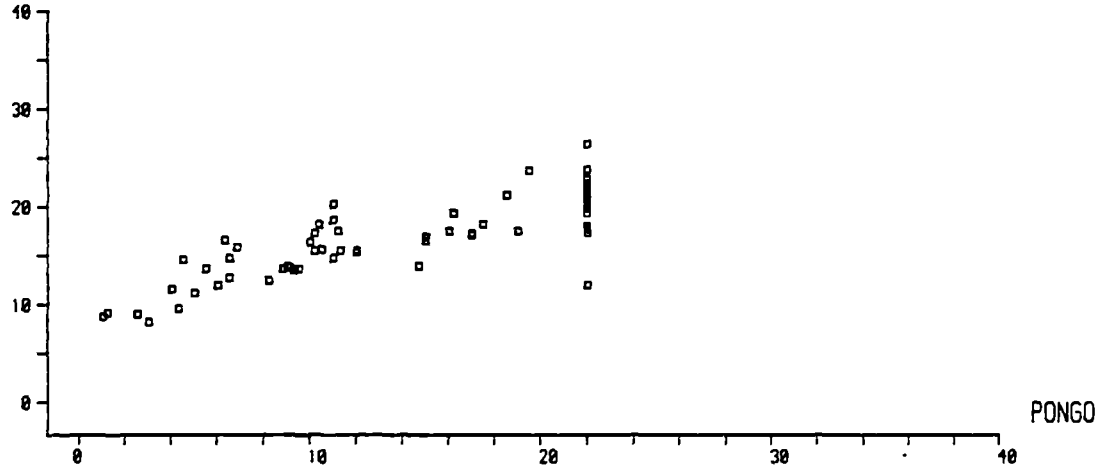
Measurement No. 3: Minimum interorbital width - MO - MO, Figure 19

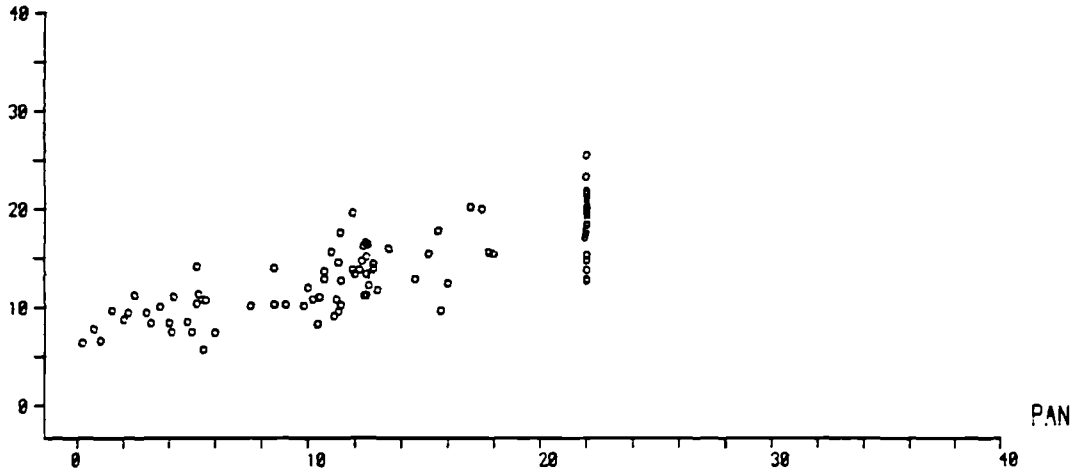
Pan, Pongo and Gorilla

This measurement approximates to the total width of the ethmoid bone, and growth in this region represents the sum of growth in width of the cribriform plate of the ethmoid and growth in width of the ethmoidal air cells. In Pan the mean value of 9 for the first postnatal year approximately doubles during the growth period to reach a mean adult value of 20, whereas in Gorilla the same mean infant value (9), nearly trebles to an adult mean of 25. In contrast, the mean value for the first postnatal year in Pongo is only 7 and little increase in growth occurs until about 10 years, after which time there is a rapid increase to an adult mean value of 13, which is approximately

Figure 18. NA - FC







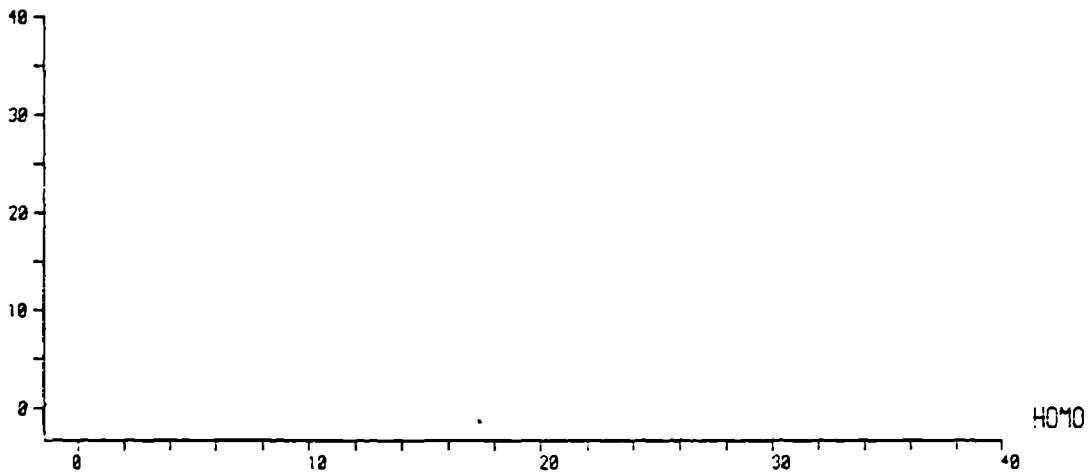
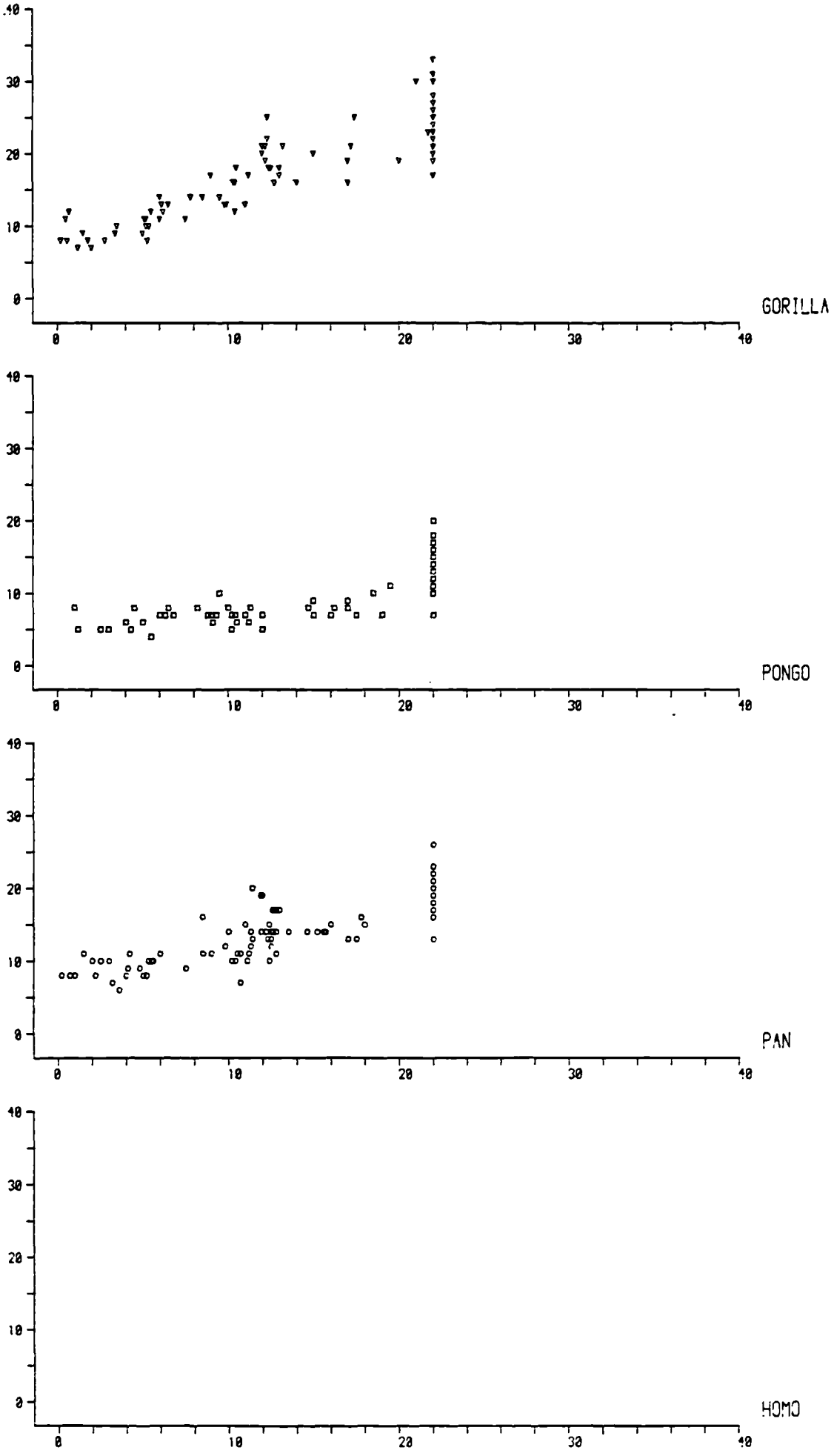


Figure 19 MO – MO



double that of the mean infant value.

Measurement No. 25: Length of the cribriform plate - FC - CL, Figure 20

Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 16, 14 and 16 respectively. These values are close to the mean adult values of 14, 12 and 14 for these taxa. There is little indication of any growth increases occurring in the length of the cribriform plate, and the adult values suggest there may be a slight decrease in length after the first 3 years, an observation previously made on data for Homo by Ford (1958).

Measurement No. 26: Length of the ethmoid bone - FC - PS, Figure 21

Pan, Pongo and Gorilla

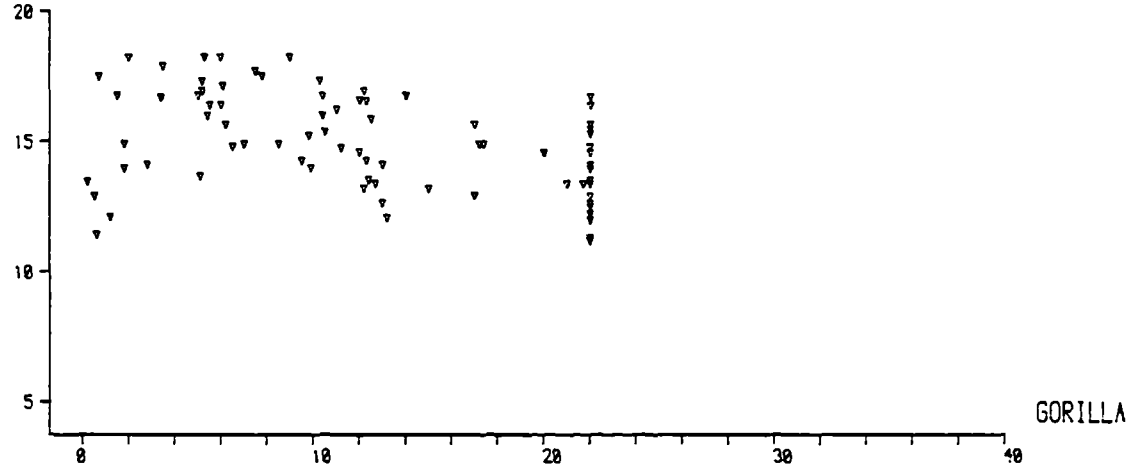
This measurement represents the total length of the ethmoid bone from the foramen caecum to the presphenoidal suture and incorporates the length of the cribriform plate and posterior ethmoidal air cells in the anterior cranial fossa. This measurement is identical to Measurement 25 in Pongo as no distinction could be made between length of the ethmoid bone and length of the cribriform plate. Growth in length of the ethmoid is greater in Pan than Gorilla, the mean values for the first postnatal year being 19 and 20 respectively, and the mean adult values 25 and 19. However, values within the adult range are present in both Pan and Gorilla soon after birth.

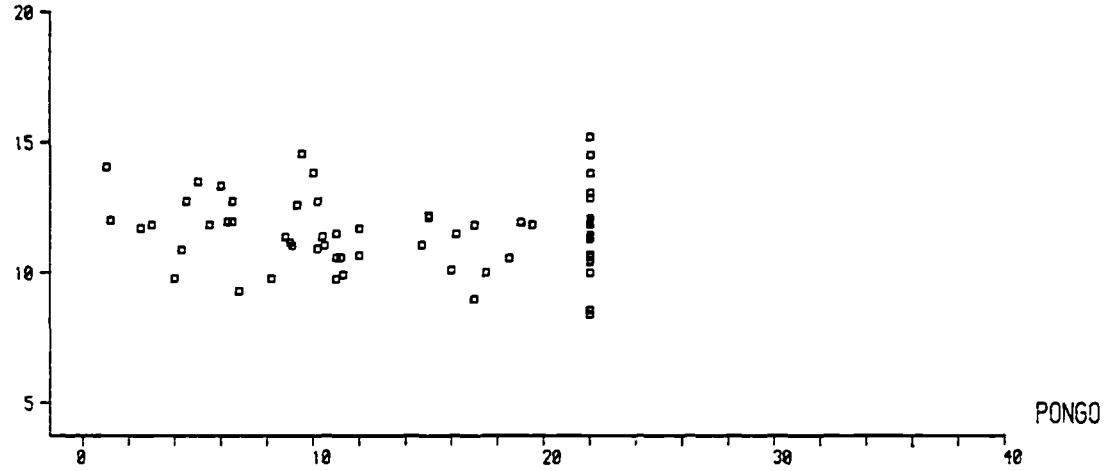
Measurement No. 30: Width of the cribriform plate - CR - CR, Figure 22

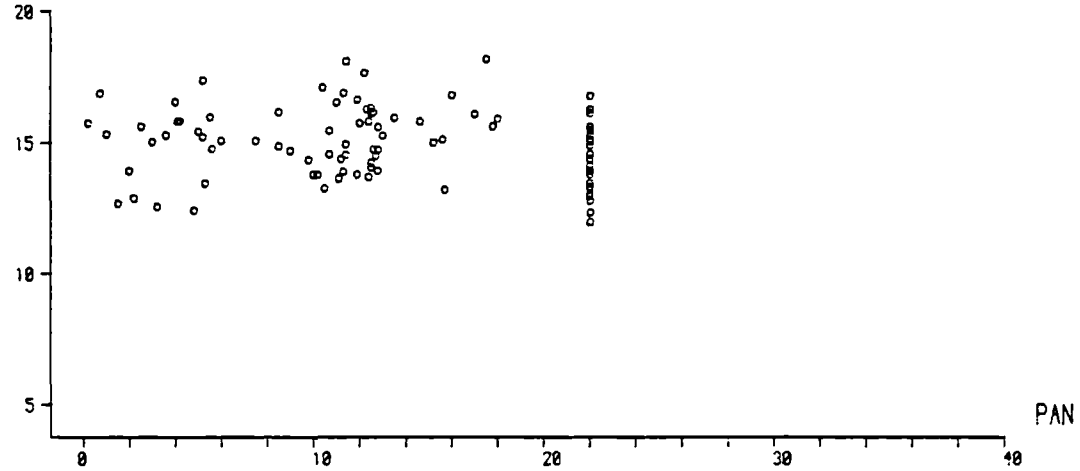
Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 6, 8 and 7 respectively. These values correspond closely with the mean adult values of 7, 9 and 9. There is then no increase in the width of

Figure 20 FC - CL







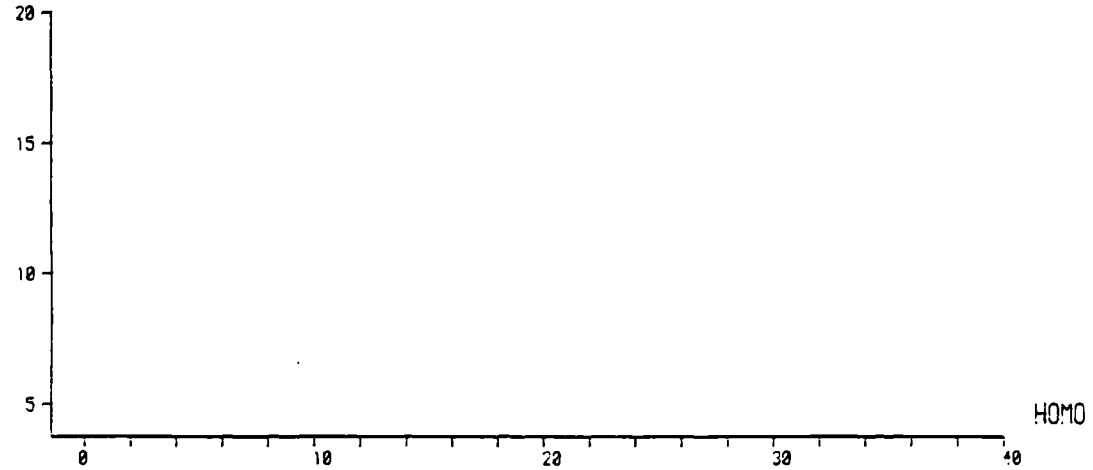
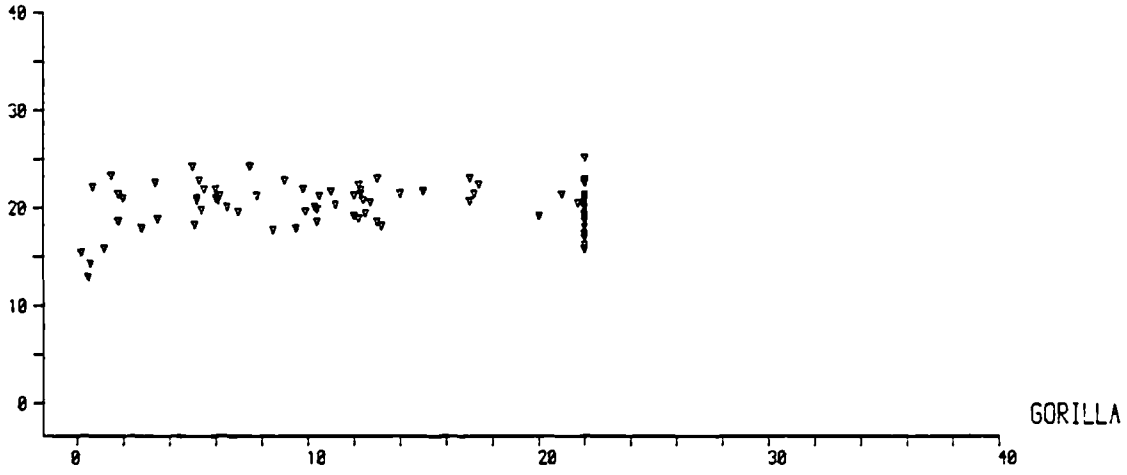
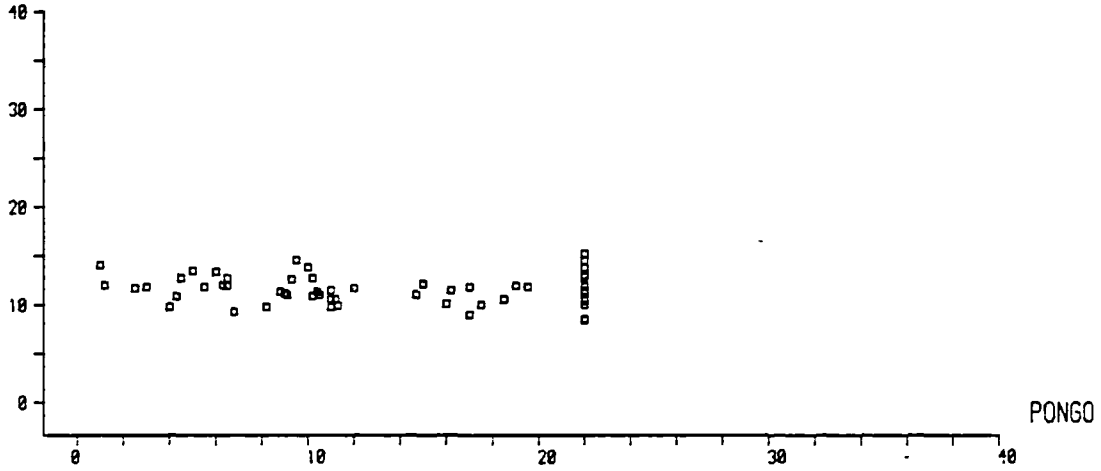
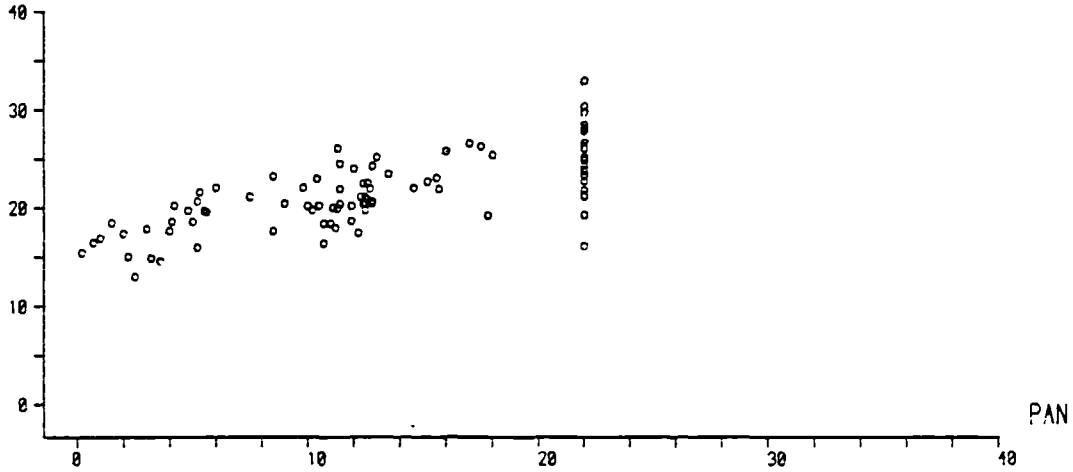


Figure 21 FC - PL







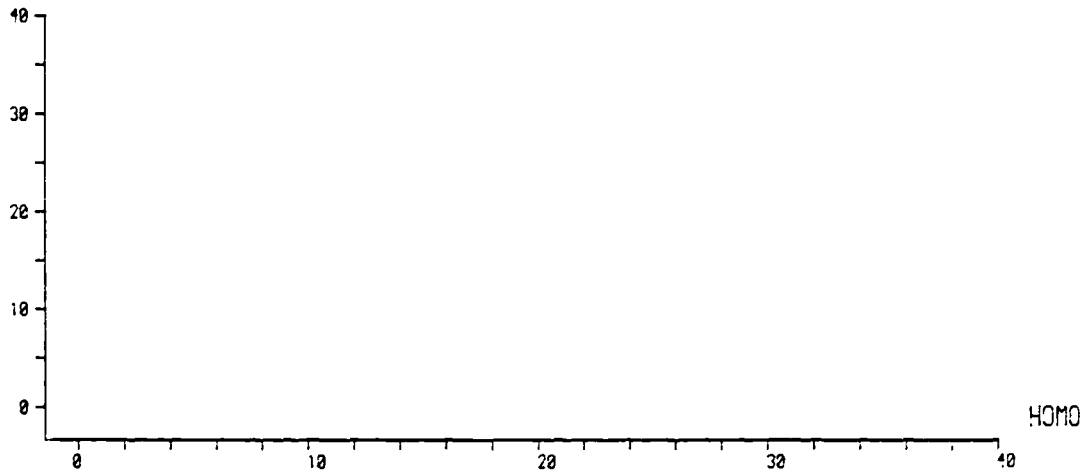
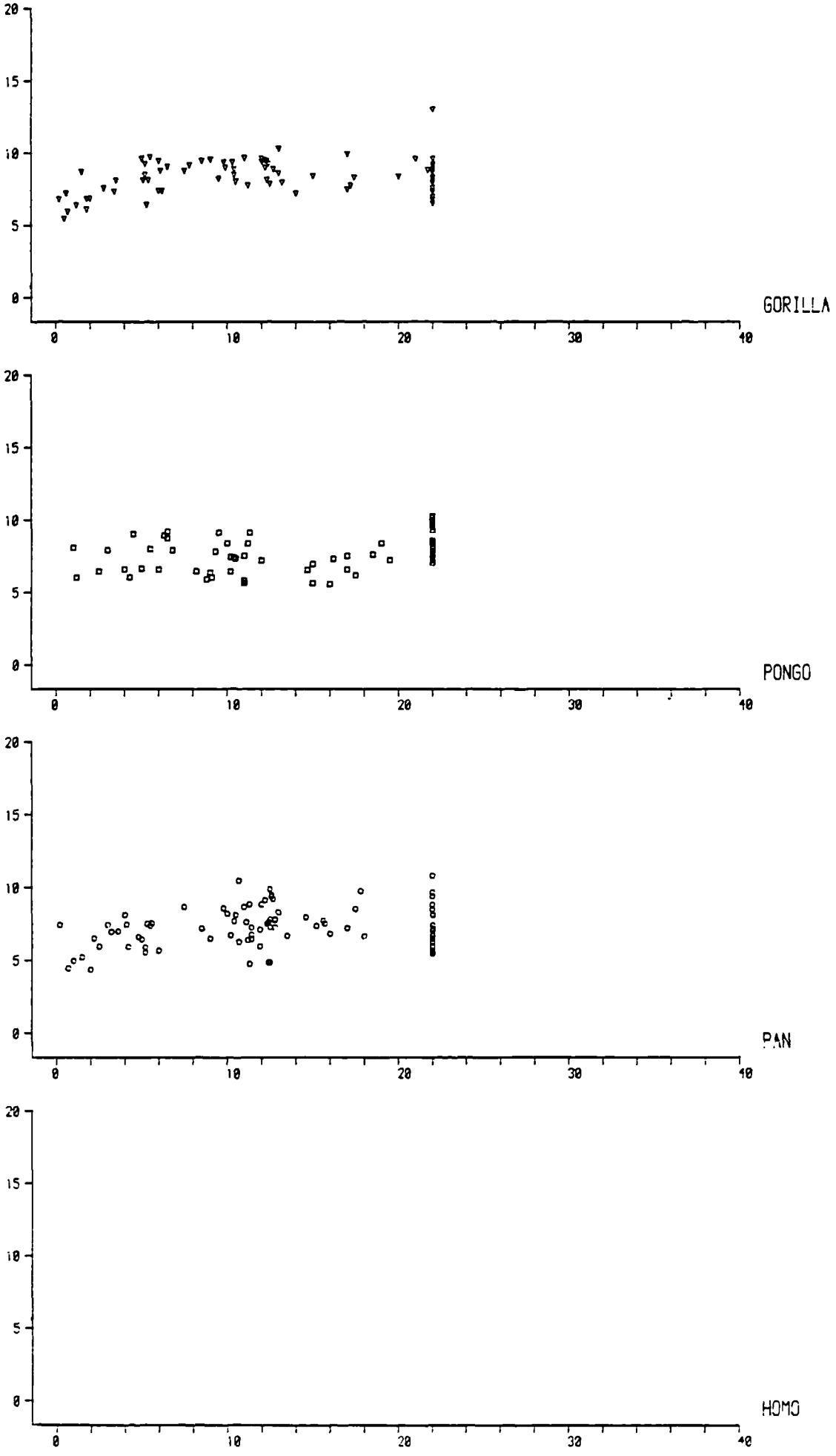


Figure 22 CR - CR



the cribriform plate after birth in any of the pongid taxa and adult values are present during the first postnatal year.

Summary of growth in the region of the ethmoid bone in the pongids

In all three taxa there is little or no growth in the length and width of the cribriform plate of the ethmoid bone after the first year. Any increase in length of the ethmoid bone appears to occur because of growth in the posterior ethmoidal air cells and is absent in the orang utan, small in the gorilla and most marked in the chimpanzee. Increase in width of the ethmoid appears to occur in all three pongids, the mean value during the first year after birth doubling in the chimpanzee and orang utan, but almost trebling in the gorilla. Interestingly, almost all this increase in the orang utan occurs just before or during the adult period. Growth of the frontal bone in the region of the ethmoid also approximately doubles during the growth period in Pan and Pongo and nearly triples in Gorilla. This continues regularly throughout the growth period in all three pongid taxa.

SECTION THREE

Growth changes in the sphenoid bone

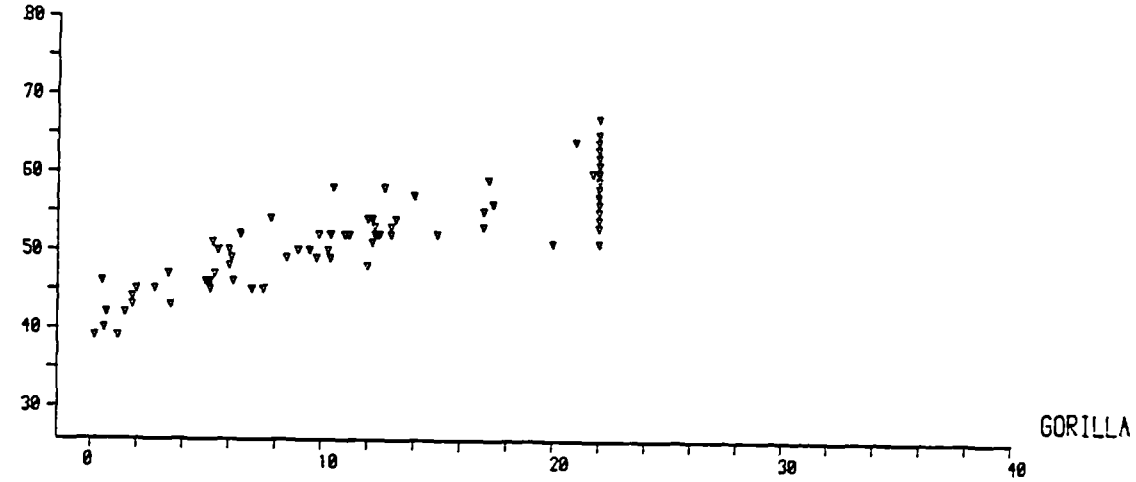
Seven linear measurements and one angular measurement involving the sphenoid bone were made on the three pongid taxa. These were measurements 4, 5, 16, 17, 18, 19, 27 and 28. In addition to these measurements made on the pongid crania, two measurements, 4 and 5, were made on the sample of Homo sapiens crania.

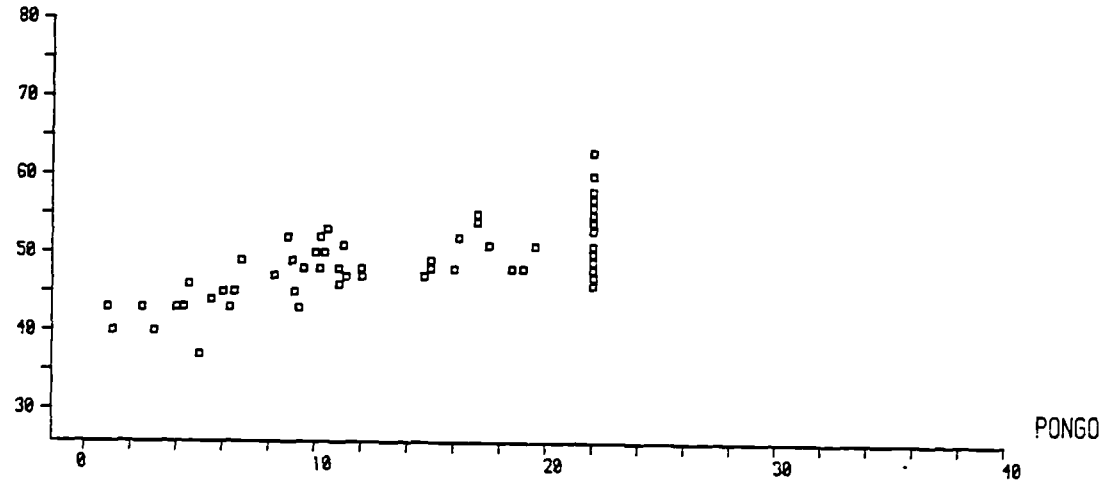
Measurement No. 4: Bi-infratemporal crest width - IT - IT, Figure 23

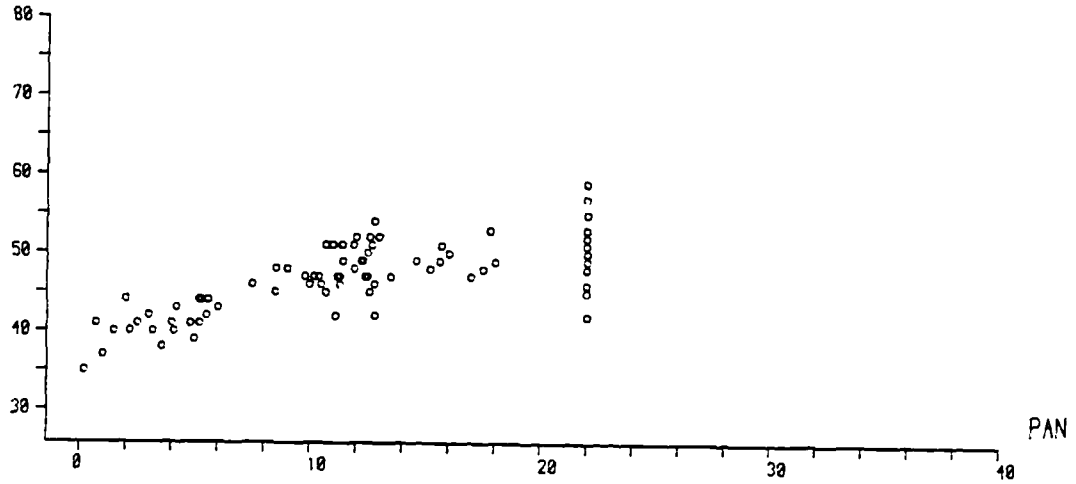
Pan, Pongo and Gorilla

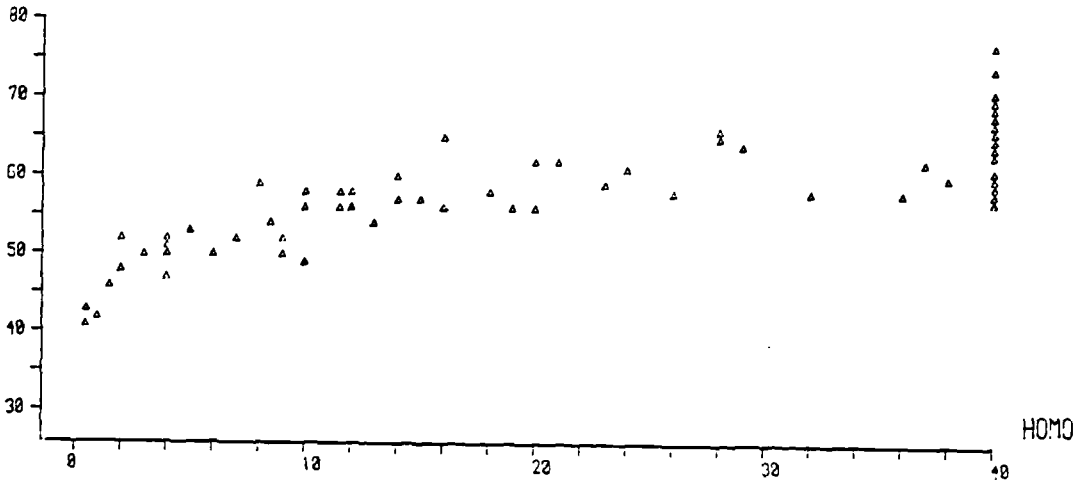
The mean values for the first postnatal year in Pan, Pongo and Gorilla are 39, 42 and 42 respectively. In all three taxa, increase in growth is

Figure 23 IT - IT









regular throughout the whole growth period and the mean adult values of 51, 52 and 59 demonstrate that the values for Gorilla increase slightly more than those for Pan and Pongo.

Homo

The mean value of 45 for the first postnatal year (about the same as Gorilla and Pongo) increases rapidly to 51 at the beginning of the second postnatal year. Values within the adult range appear during the fourth year but from two years to adulthood over a period of 18 years there is a very gradual increase to an adult mean value of 66. This represents a rate of growth of less than 1 mm/year in all, whereas for example in Gorilla, although the adult mean value is considerably less, the growth rate is approximately 2 mm/year, twice the rate which occurs in Homo sapiens.

Measurement No. 5: Bi-foramen ovale width - FO - FO, Figure 24

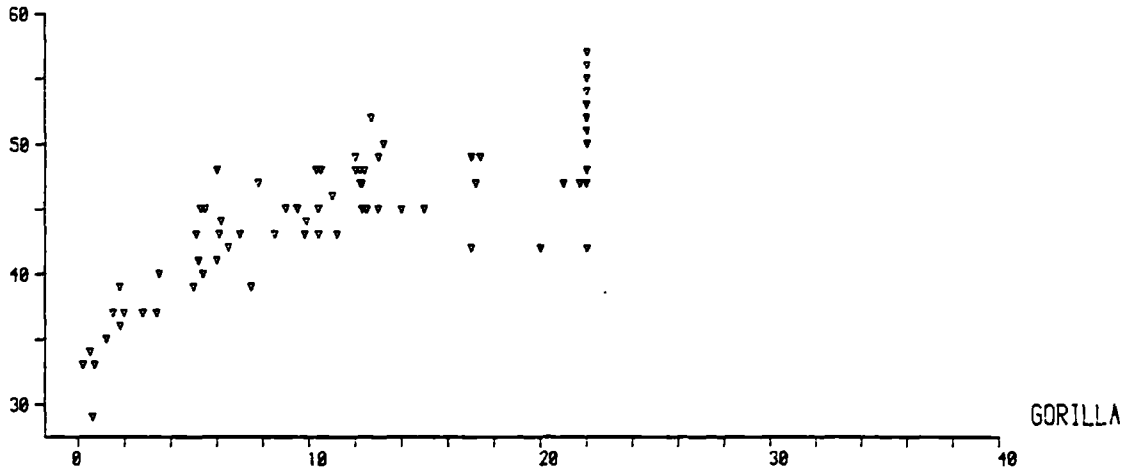
Pan, Pongo and Gorilla

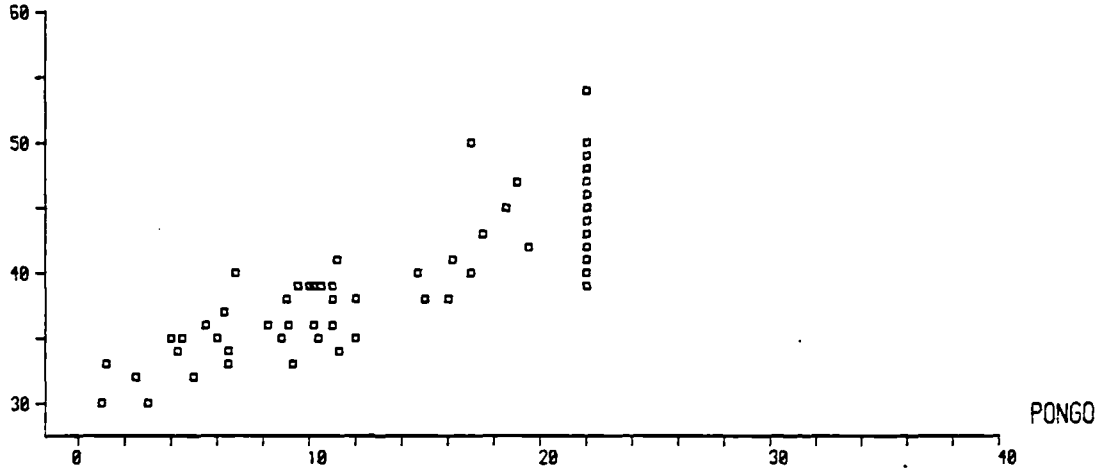
The mean values for the first postnatal year in Pan, Pongo and Gorilla are 32, 32 and 35 respectively. These increase regularly during the growth period to adult mean values of 43, 45 and 51, the increase in Gorilla being greater.

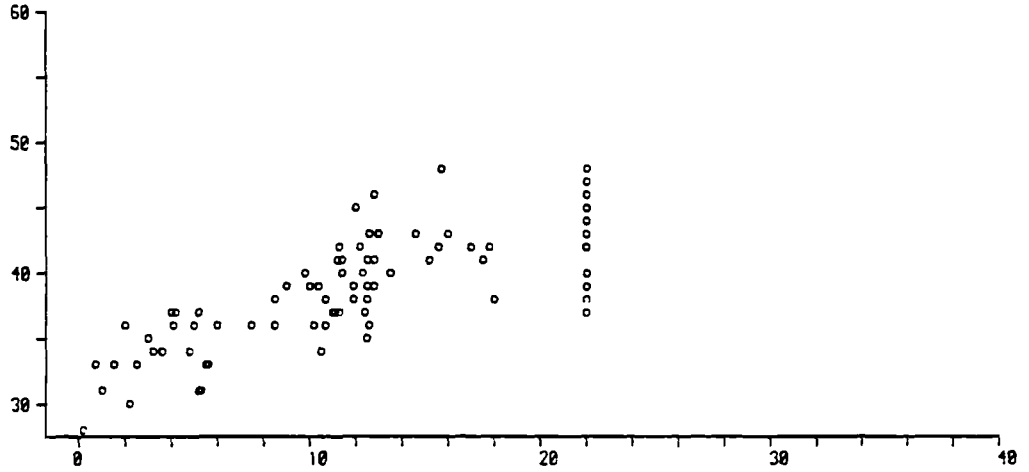
Homo

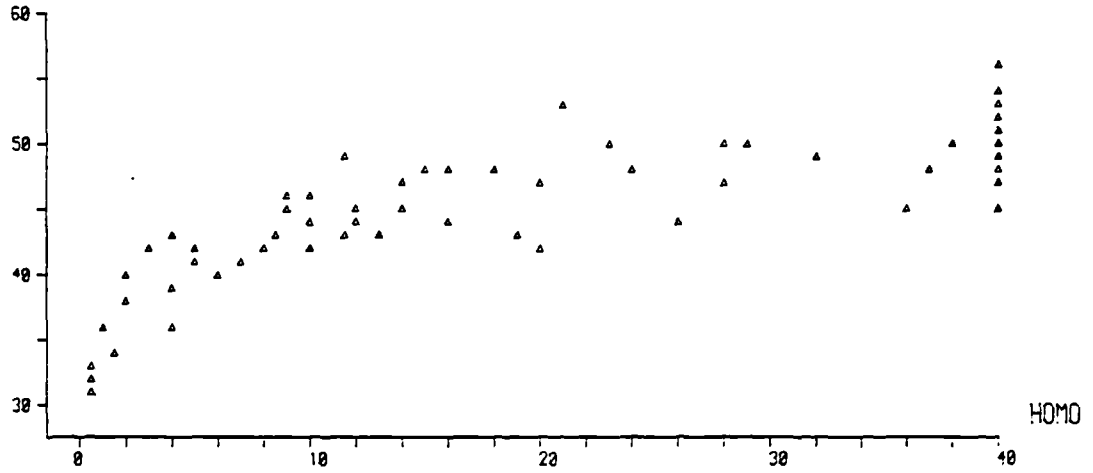
The mean value of 35 for the first postnatal year rises rapidly to a mean of 40 during the second postnatal year. Hereafter, there is a very gradual increase to an adult mean of 50 over a period of 18 years. Values within the adult range appear about the fifth year. Once again, this represents an overall average growth rate of approximately half that

Figure 24 FO - FO









of the three pongid taxa, despite the early rapid increase in growth rate in Homo.

Measurement No. 16: Bi-optic canal width - OC - OC, Figure 25

Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan. Pongo and Gorilla are 16, 13 and 16 respectively. These increase to mean adult values of 26, 22 and 31. The growth curve in Pongo bears some resemblance to that of Measurement No. 3 (MO - MO), Figure 19, where values for Pongo are again the smallest of the three pongid taxa, and in this too the main increase in width appears to occ ur more towards the end of the growth period.

Measurement No. 17: Bi-superior orbital fissure width - SOF - SOF, Figure 26

Pan. Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 28, 31 and 27 respectively. These rise to mean adult values of 37, 40 and 38, representing similar growth increments in all three taxa.

Measurement No. 18: Bi-pterion width - PT - PT, Figure 27

Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 58, 65 and 57 respectively, Pongo showing higher values for width of the skull soon after birth. However, the adult mean values of 68, 68 and 70 are similar, due to the small amount of growth occurring

Figure 25 OC - OC

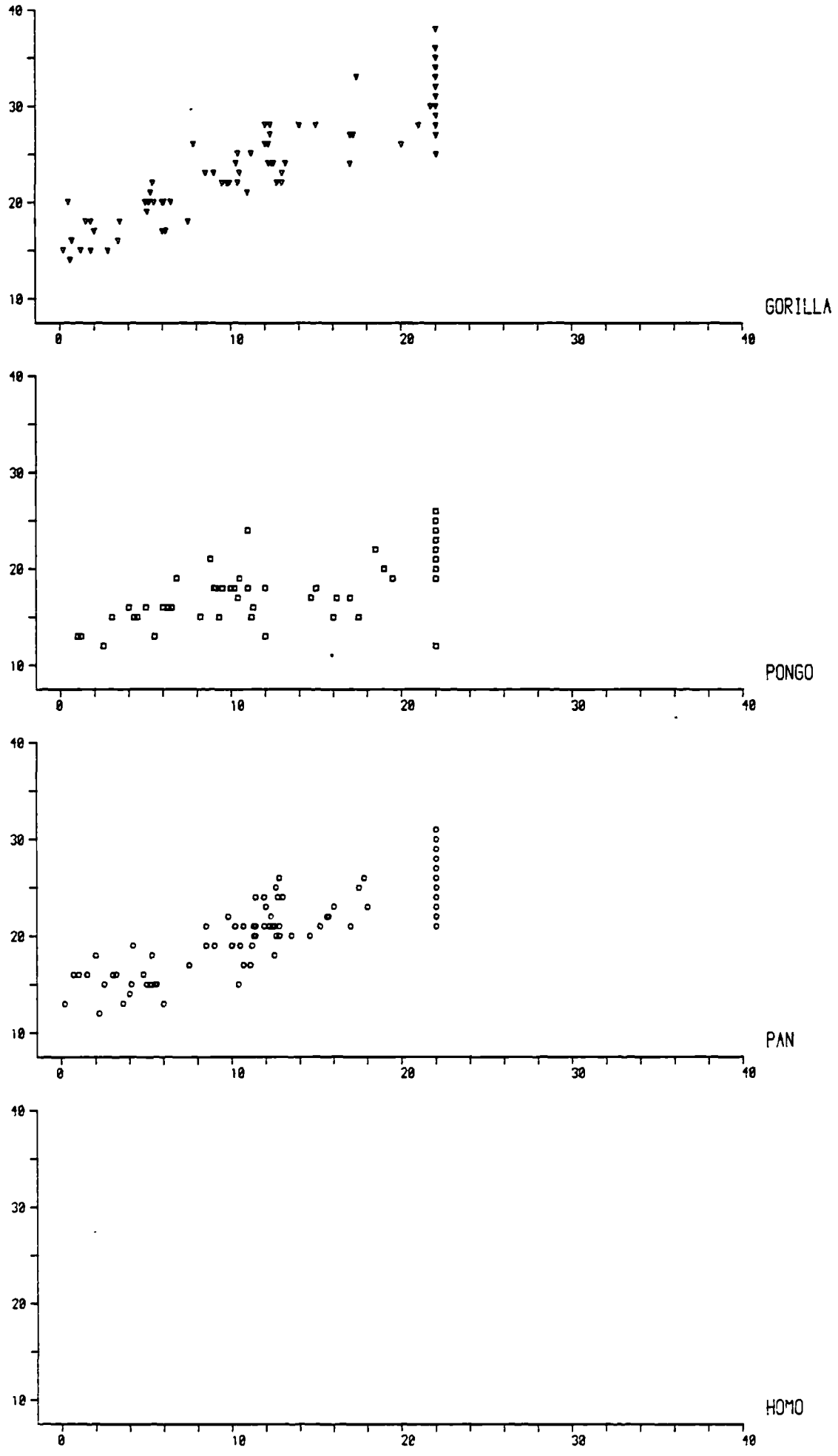
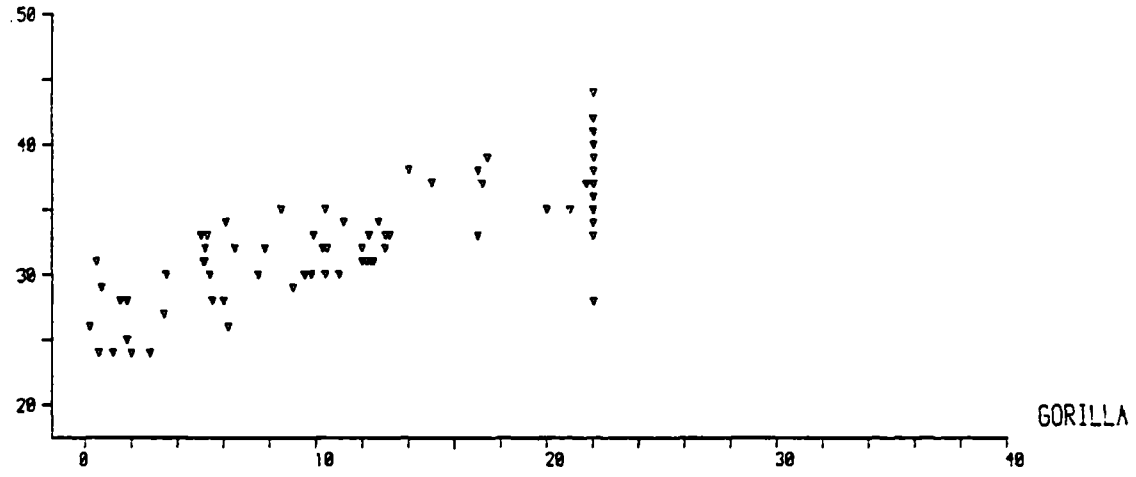
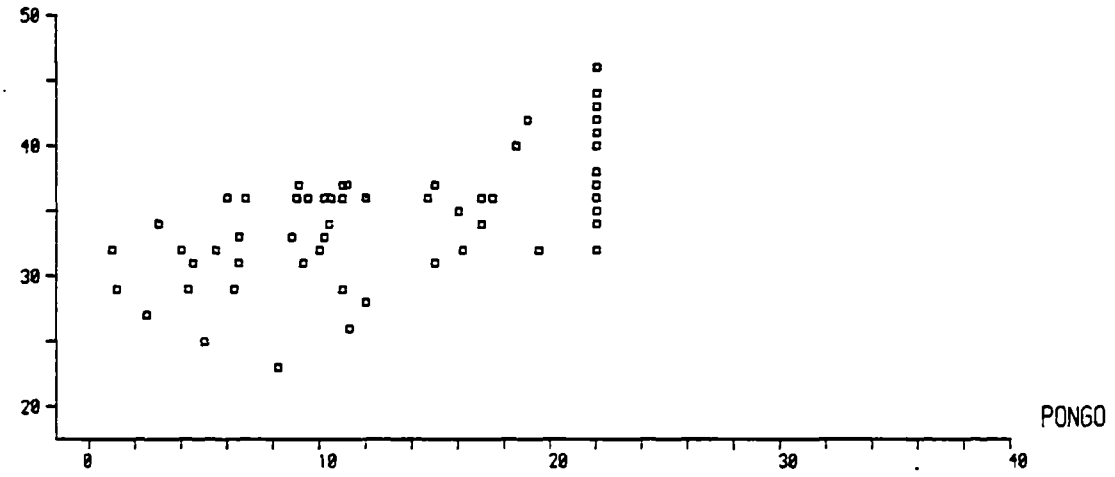
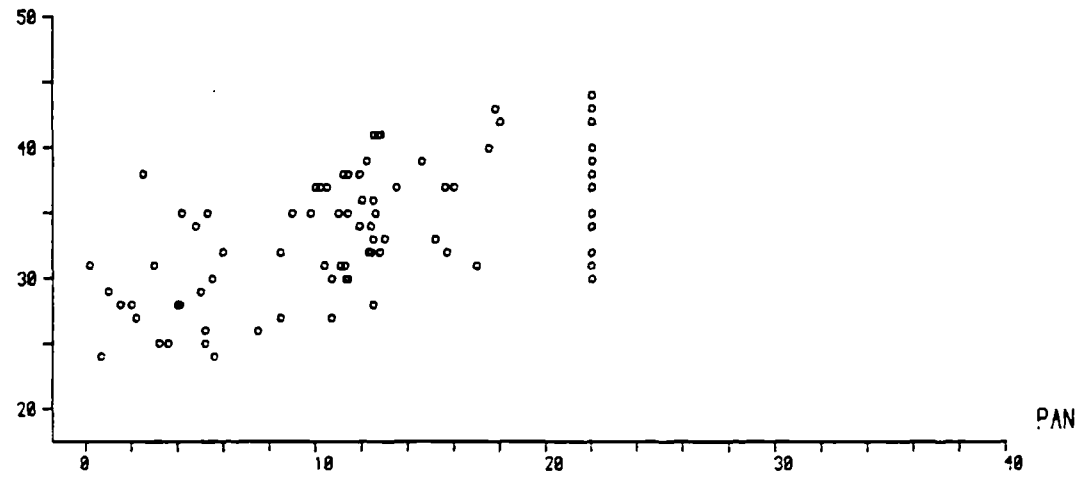


Figure 26 SOF - SOF







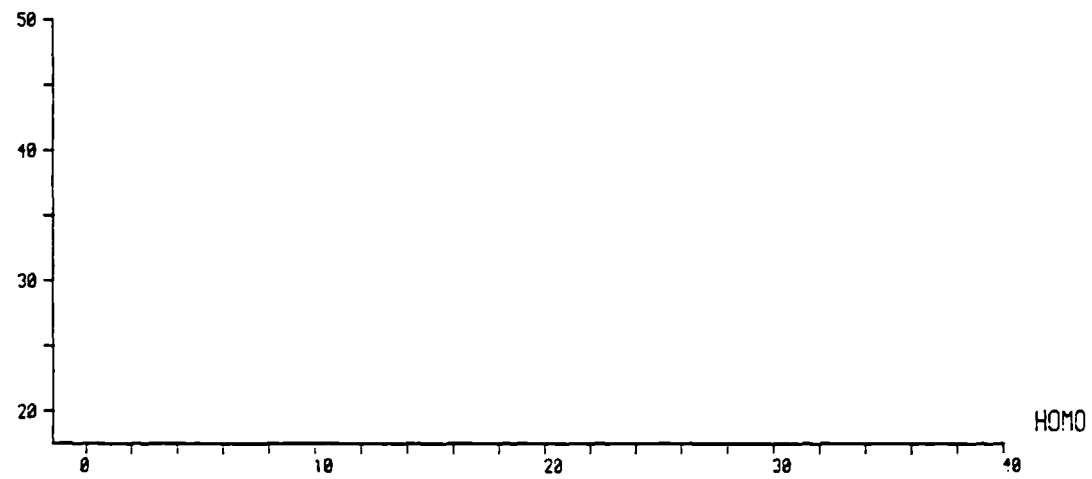
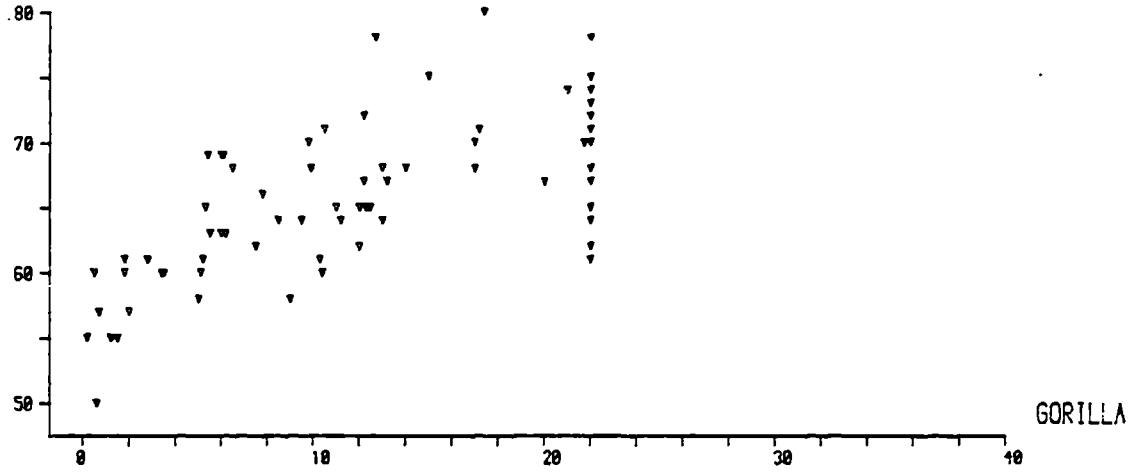
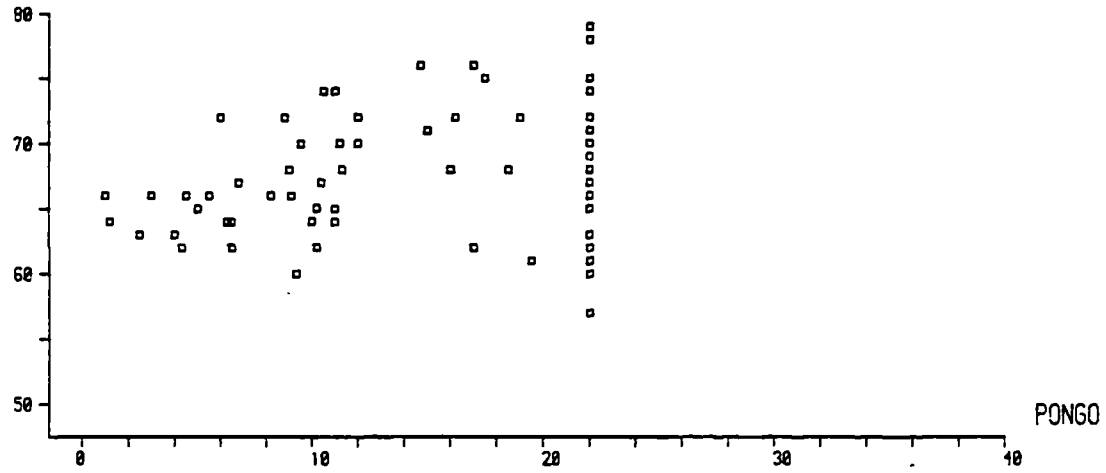
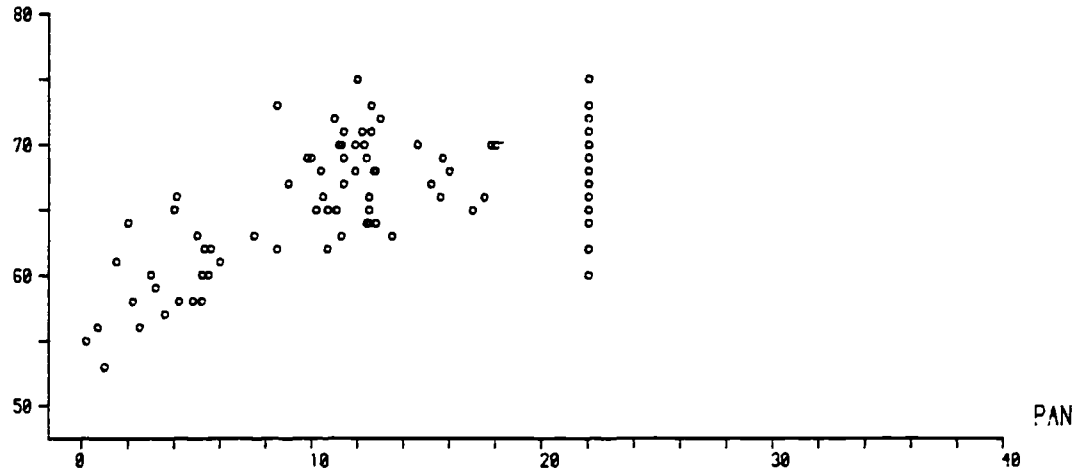
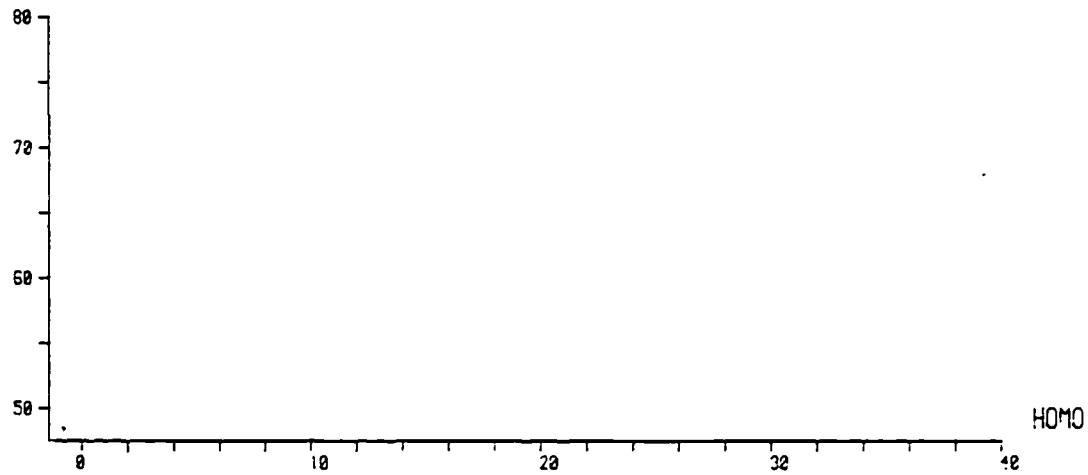


Figure 27 PT - PT









in Pongo during the growth period.

Measurement No. 19: Height of the pterygoid plate - HA - IT, Figure 28

Pan, Pongo and Gorilla

The mean values of 13, 13 and 12 respectively, for Pan, Pongo and Gorilla during the first postnatal year increase regularly throughout the total growth period to mean adult values of 27, 26 and 34. This represents a doubling in value for Pan and Pongo, but a three-fold increase for Gorilla.

Measurement No. 27: Length of the sphenoid bone - PS - SB, Figure 29

Pan, Pongo and Gorilla

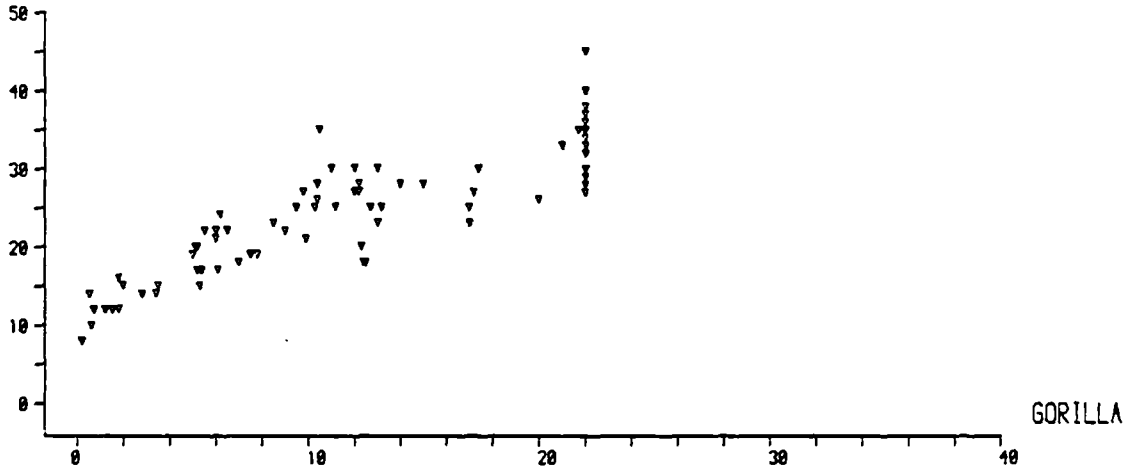
The mean value of 22 for the first postnatal year in Pan remains almost unchanged throughout the growth period, the mean adult value being 24. The mean value of 18 for the first postnatal year in Pongo rises to an adult mean of 36, so doubling in length, and the postnatal mean value of 16 in Gorilla rises to an adult mean value of 36, increasing slightly more than in Pongo, but considerably more than in Pan.

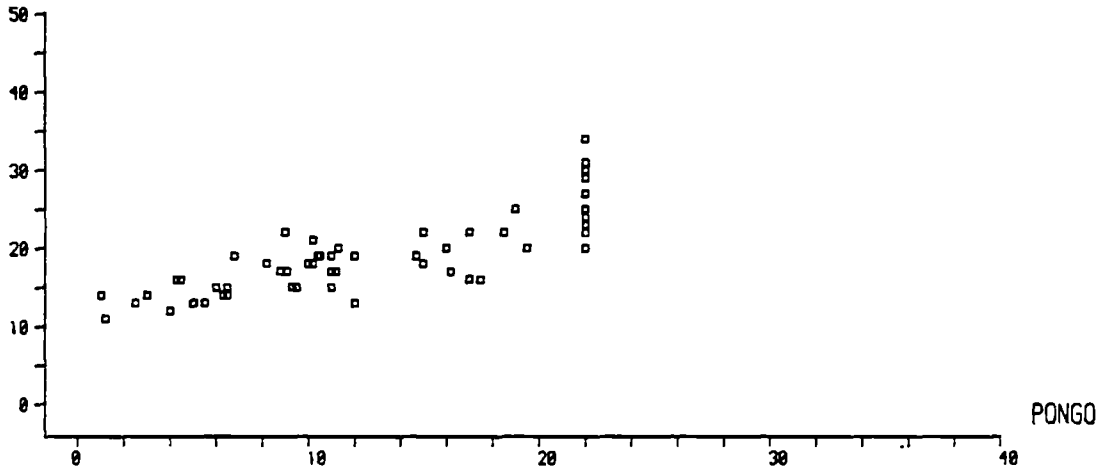
Measurement No. 28: Cranial base angle γ - FC - S - SB, Figure 30

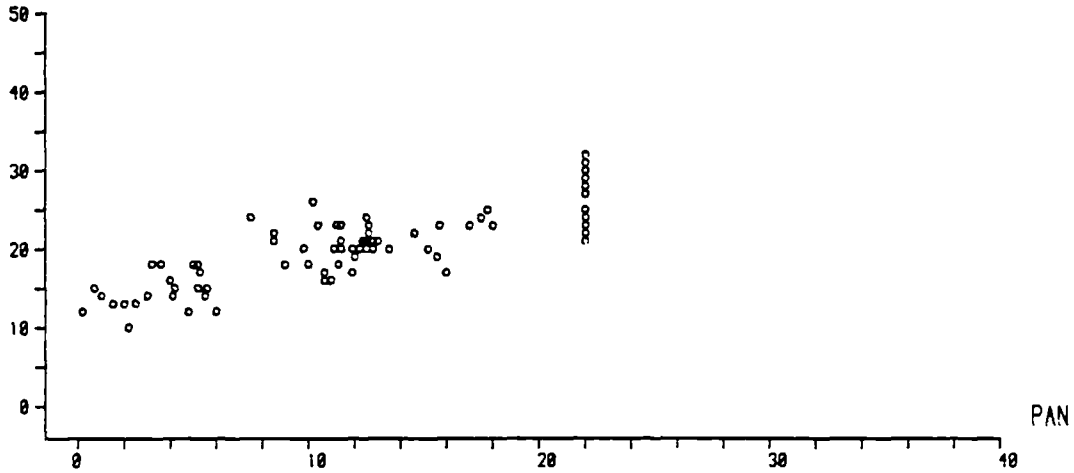
Pan, Pongo and Gorilla

The range of values for this measurement is very wide for all three pongid taxa, both for values early on during the growth period and for the

Figure 28 HA - IT







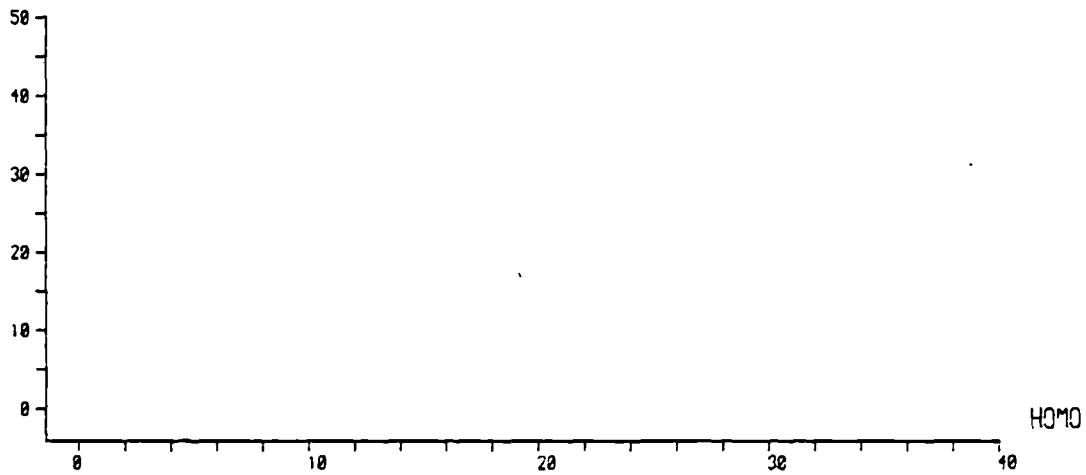
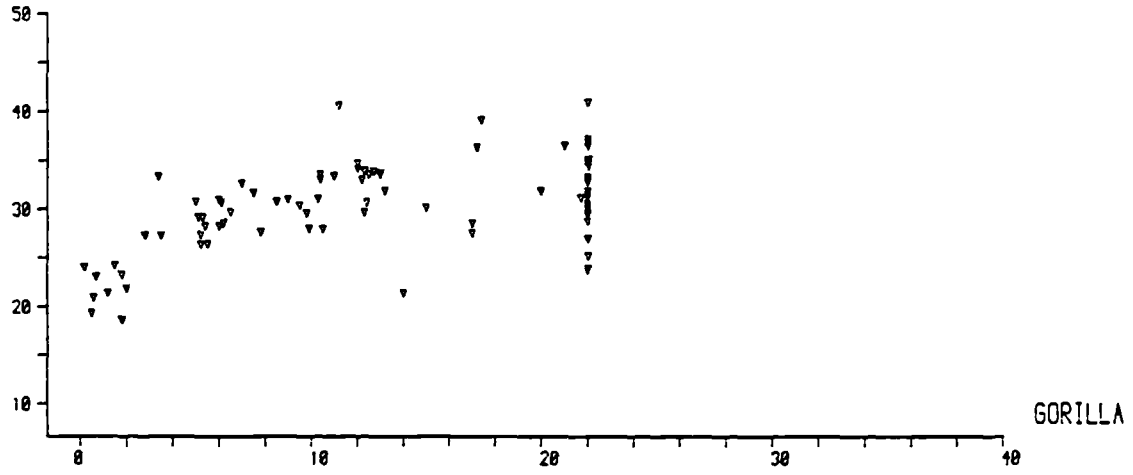
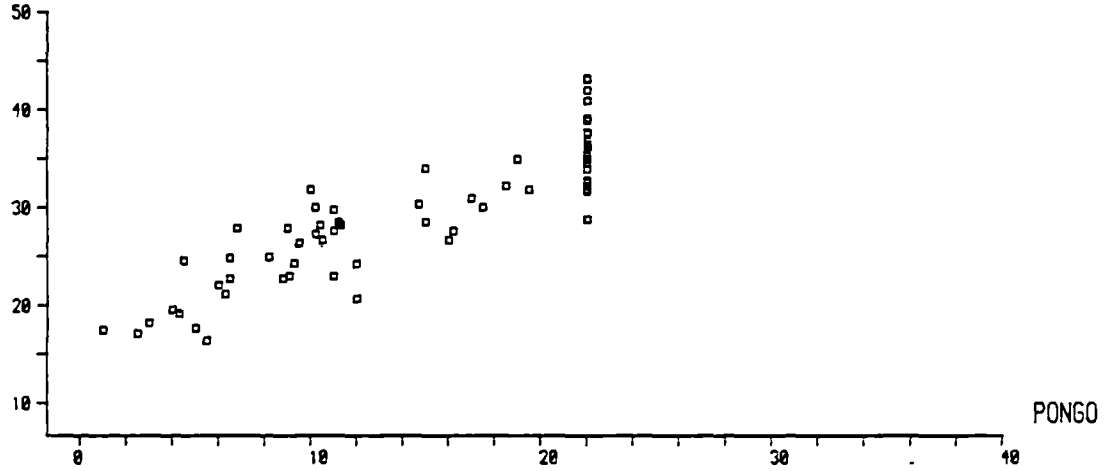
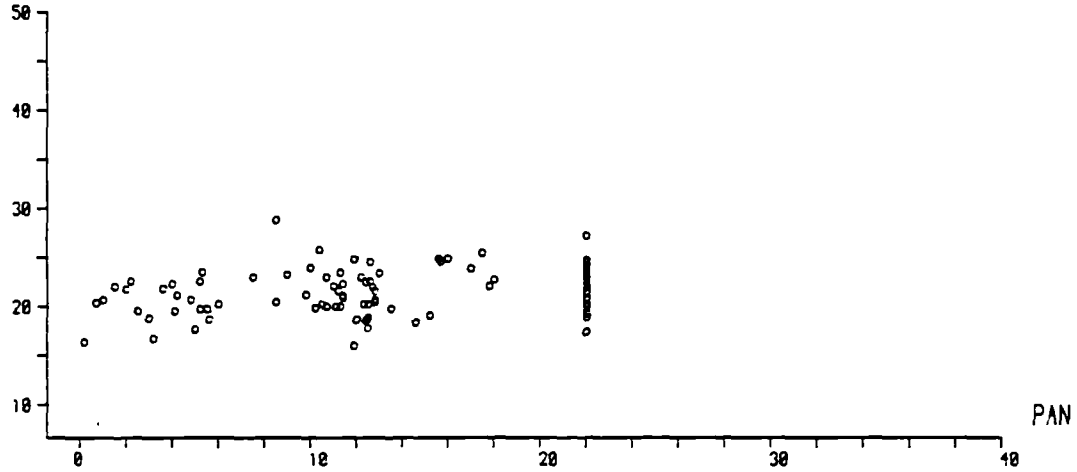


Figure 29 PS - SB







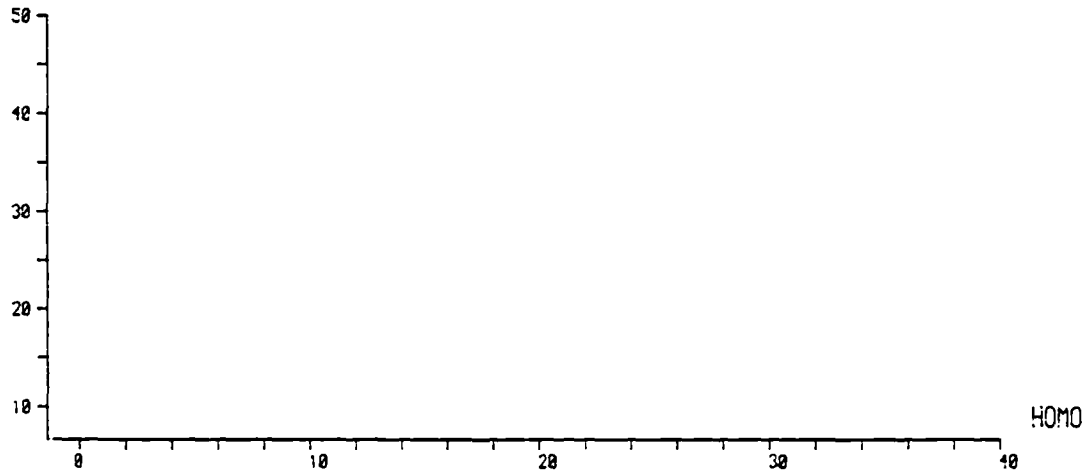
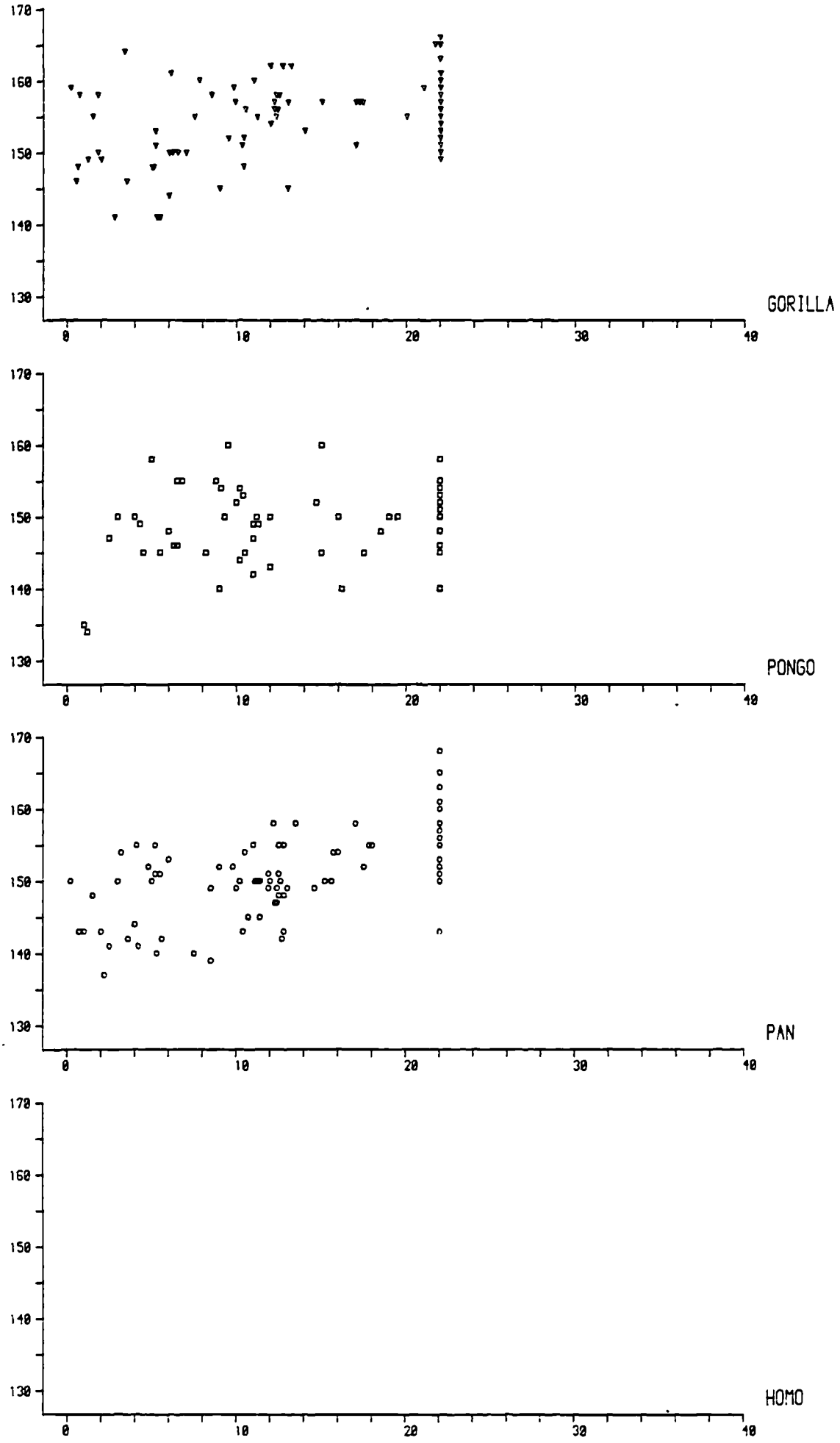


Figure 30 Angle Gamma (γ)



adult values. However, the mean values for the first postnatal year in Pan, Pongo and Gorilla are 145°, 135° and 152°. The values for Pan rise steadily during the growth period to reach an adult mean value of 156° (the range, however, is 143°- 168° and incorporates values recorded soon after birth). The low value of 135° for the mean during the first postnatal year in Pongo lies well below all the other measurements made for Pongo, for soon after birth all values fall within the adult range. The adult mean value of Pongo, 150°, is slightly less than that in Pan. The mean adult value for Gorilla is 156°, identical to Pan, but the range of values throughout the total growth period demonstrates how little this angle changes during postnatal growth.

Summary of growth of the sphenoid bone in the three pongid taxa and Homo sapiens

Growth in length of the body of the sphenoid bone appears to bear an inverse relationship to growth in length of the ethmoid bone. In Pan, there is most growth of the ethmoid and least growth of the sphenoid. In Gorilla, there is less growth of the ethmoid but more growth of the sphenoid than in Pan. In Pongo, where there is least growth in the ethmoid bone, there is most growth in the length of the sphenoid. The combined growth in length of the sphenoid and ethmoid is largely complete by the fifth or sixth year in all the pongid taxa.

Growth in height of the pterygoid plates of the sphenoid bone continues throughout the growth period. The rate in Gorilla is greater than in Pan and Pongo; the mean of the first postnatal year trebles, whereas it only doubles in Pan and Pongo.

Growth in width across the bilateral anatomical landmarks of the sphenoid bone tends to show a similar pattern of regular growth throughout the growing period with the rates and adult values in Gorilla exceeding on average the rates and adult values in Pan and Pongo. The bi-infratemporal

crest (IT - IT), bi-superior orbital fissure (SOF - SOF) and bi-pterion (PT - PT) measurements stand out as attaining adult values earlier in the growth period than the bi-foramen ovale and bi-optic canal measurements, which only begin to attain adult values after five years or so. Two growth patterns that stand out are the bi-pterion width in Pongo that attains adult dimensions extremely quickly by the first postnatal year, and the bi-infra-temporal crest measurement in Gorilla that takes three or four years longer than Pan and Pongo before values fall within the adult range.

The cranial base angle in the three pongid taxa shows a slight increase, but this is not at all marked and is greatly overshadowed by the wide adult range that exists in all three taxa. Pan shows a more obvious trend in this increase throughout the growth period, but Pongo by far the most marked increase after the first postnatal year, due entirely to two very low values which must be regarded with some caution.

The pattern in Homo sapiens is quite distinct in both measurements made. There is an early rapid period of growth, much more pronounced than in any of the pongid taxa, but a much reduced growth rate after the first year or so, which continues for 19 years over a much extended growth period. The result is a larger adult mean value for bi-infratemporal crest and bi-foramen ovale width in Homo than those in the pongid taxa. The only exception is that the mean bi-foramen ovale width in Gorilla (51) just exceeds that of Homo (49).

SECTION FOUR

Growth changes in the temporal bone

Nine measurements were made on the temporal bone of both Homo sapiens and the three pongid taxa; five bilateral measurements of width (Nos. 6, 7, 8, 11 and 12), two linear (Nos. 14 and 15) and two angular (Nos. 31 and 32).

Measurement No. 6: Bi-carotid canal width - CC - CC, Figure 31

Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 30, 33 and 32 respectively. Values within the adult range appear earlier, at about 3 years, in Pongo and Gorilla than they do in Pan, where they appear at about 5 years. Growth seems to level off around 8 years and the adult mean values of 43, 50 and 47 represent a similar growth increase in all the three taxa.

Homo sapiens

The mean value of 34 for the first postnatal year rises steeply to include values within the adult range at $2\frac{1}{2}$ years. After this time, there is a very gradual increase to an adult mean of 57 over the extended growth period of 18 years.

Measurement No. 7: Bi-petrous temporal apex breadth - PA - PA, Figure 32

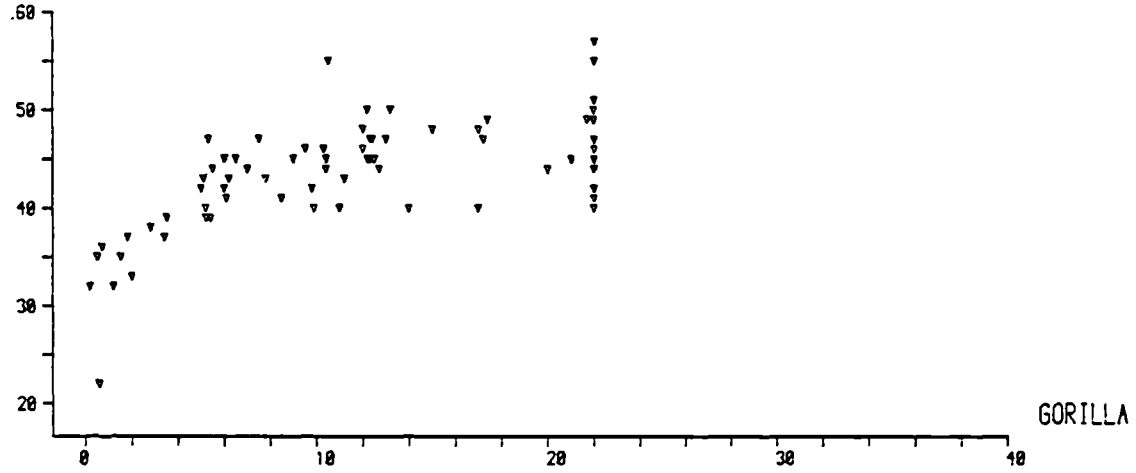
Pan, Pongo and Gorilla

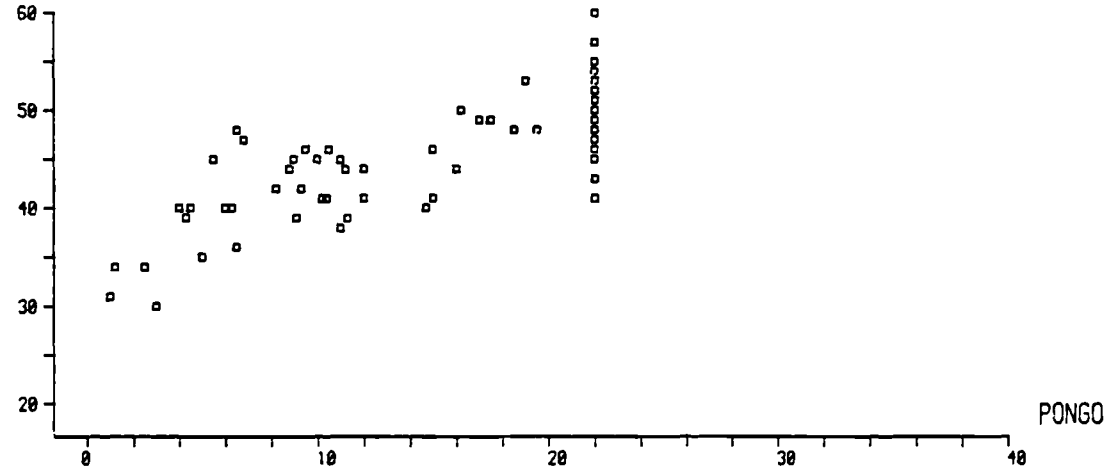
The mean values for the first postnatal year in Pan, Pongo and Gorilla are 12, 16 and 15 respectively. These rise gradually throughout the growth period to adult mean values of 24, 29 and 30, doubling in width in all three taxa.

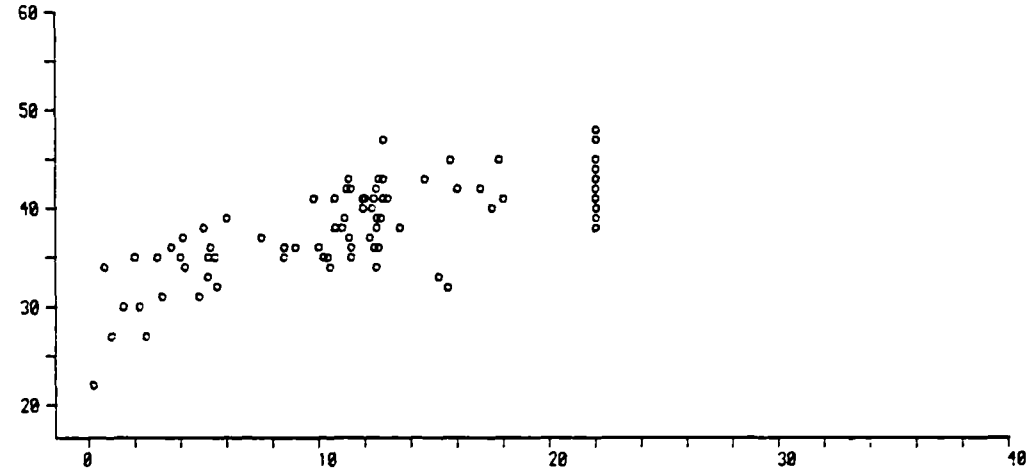
Homo sapiens

The mean value of 17 during the first postnatal year rises to include values of 28 (i.e. within the adult range) at 5 years, after which time there is a very gradual increase to an adult mean value of 32 over the remaining growth period.

Figure 31 CC - CC







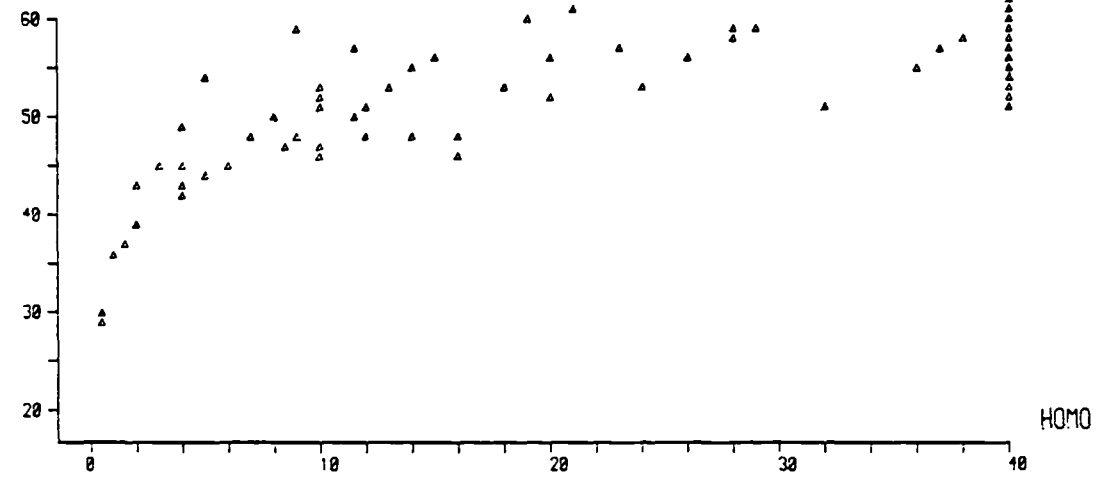
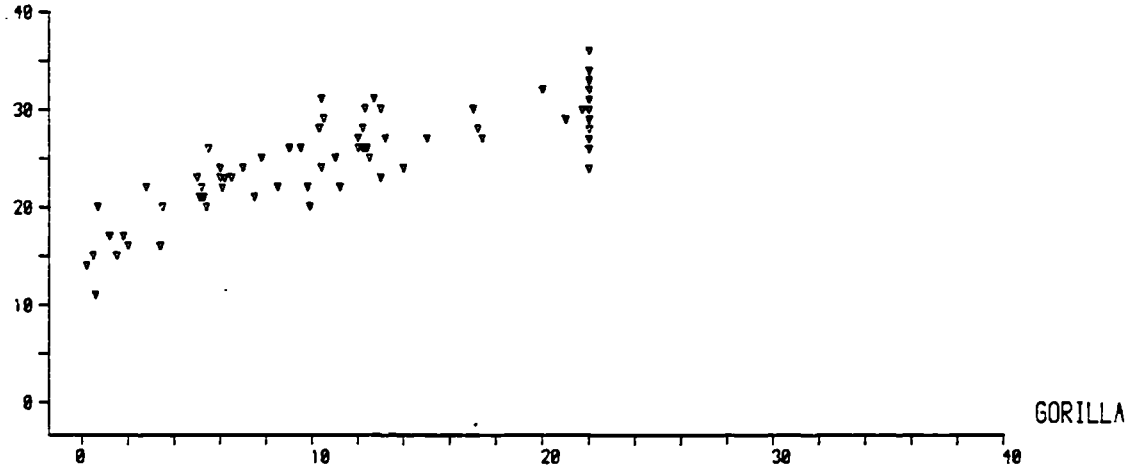
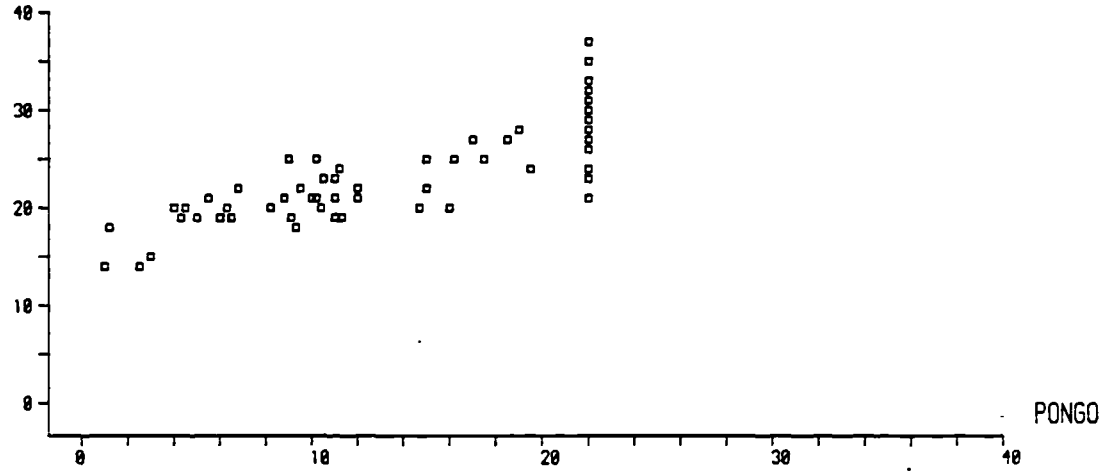
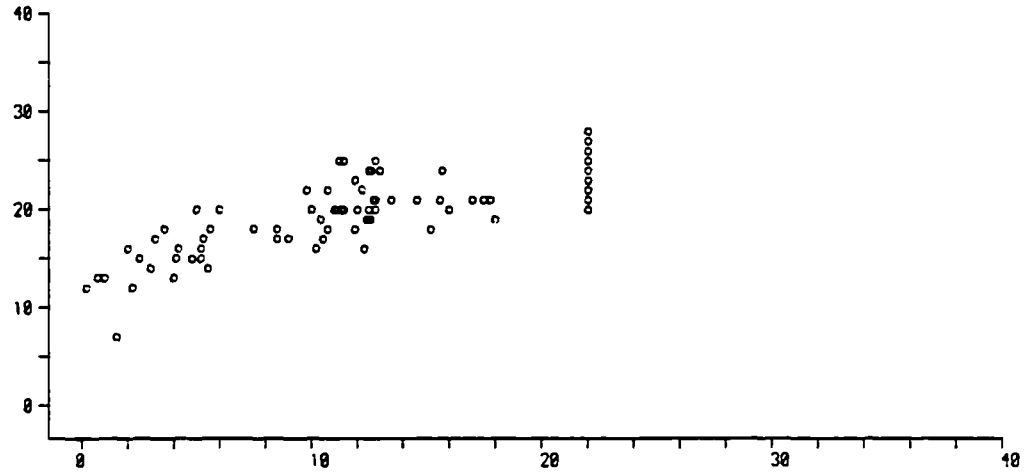
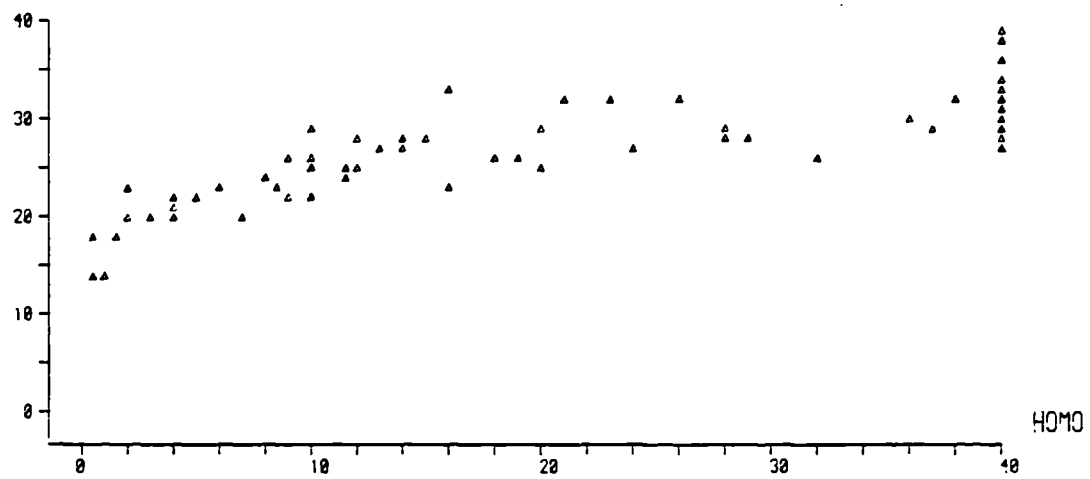


Figure 32 PA - PA









Measurement No. 8: Bi-tympanic plate width - TP - TP, Figure 33

Pan, Pongo and Gorilla

The mean values for Pan, Pongo and Gorilla during the first postnatal year are 54, 68 and 62 respectively. These rise steeply (like Measurement No. 2, maximum width of the cranium) to mean adult values of 104, 118 and 132, once again roughly doubling in width during the growth period, but increasing least in Pongo.

Homo sapiens

During the first postnatal year there is a tremendous spurt of growth from about 38 to 68. After this time, there is a gradual increase to an adult mean value of 99, with values within the adult range appearing for the first time at $4\frac{1}{2}$ years.

Measurement No. 11: Bi-styloid pit width - SP - SP, Figure 34

Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 47, 47 and 48 respectively. Growth occurs more rapidly in Gorilla during the first 4 years, but mean adult values of 59, 68 and 65 demonstrate that more increase in width occurs in Pongo during the total growth period.

Homo sapiens

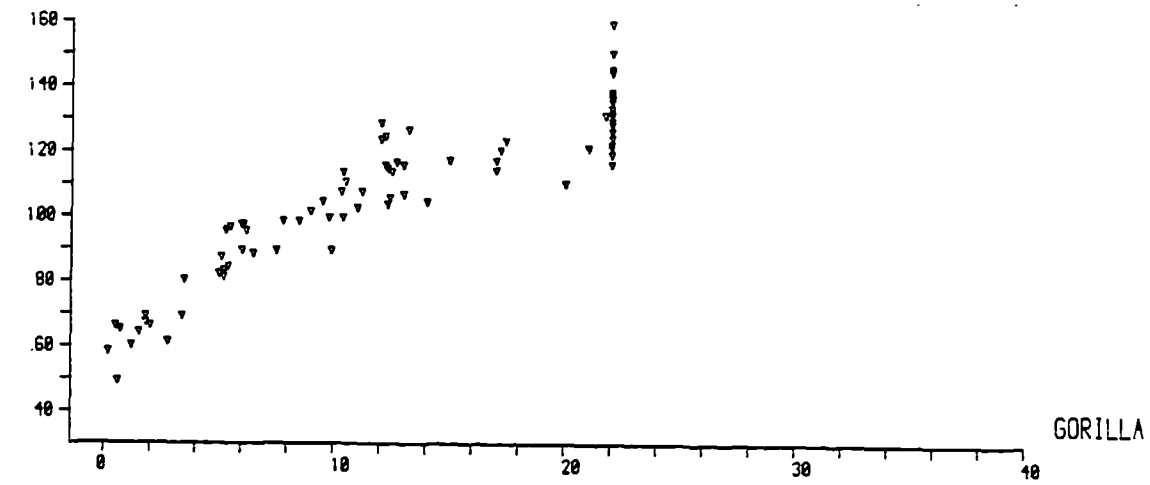
During the first year there is increase from 30 to 60 and after this time, only a very gradual increase to an adult mean of 78. Values within the adult range appear at about 3 years of age.

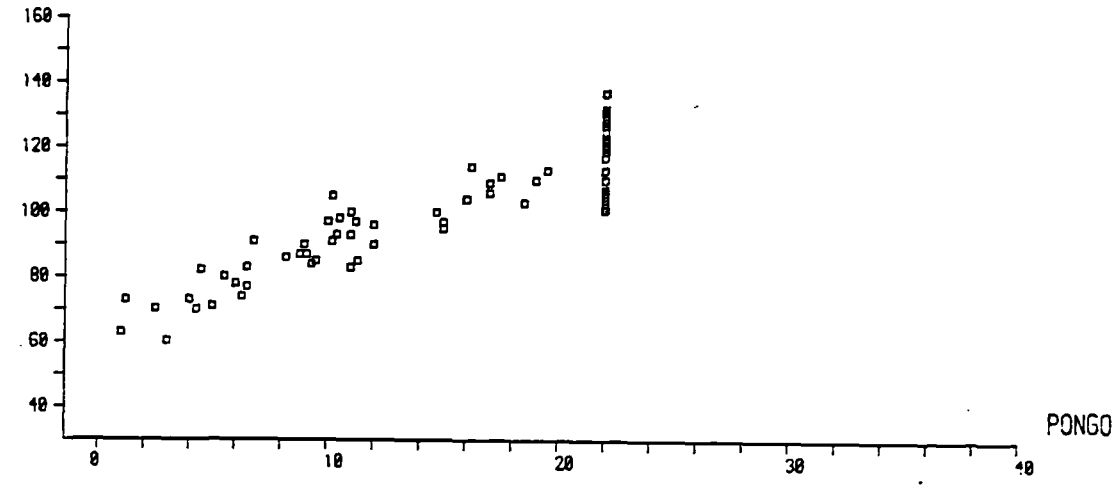
Measurement No. 12: Bi-stylomastoid foramen width - SM - SM, Figure 35

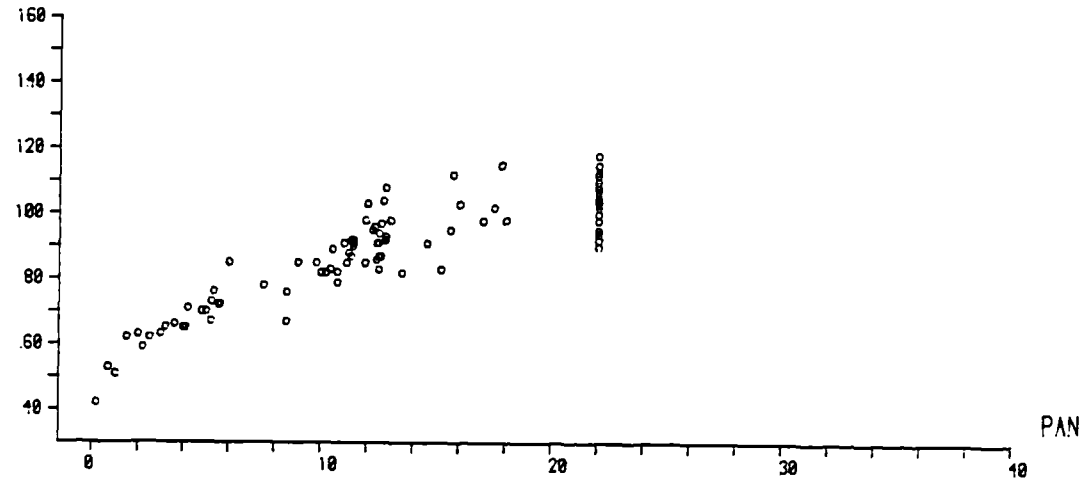
Pan, Pongo and Gorilla

The growth patterns of this curve are very similar to the preceding one for Measurement No. 11 (SP - SP). The mean values for the first postnatal

Figure 33 TP - TP







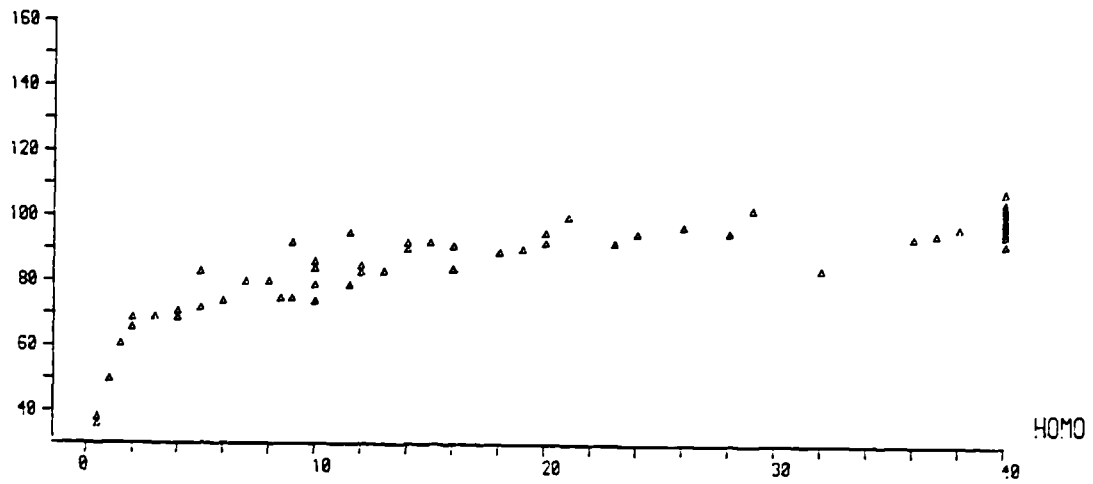


Figure 34 SP - SP

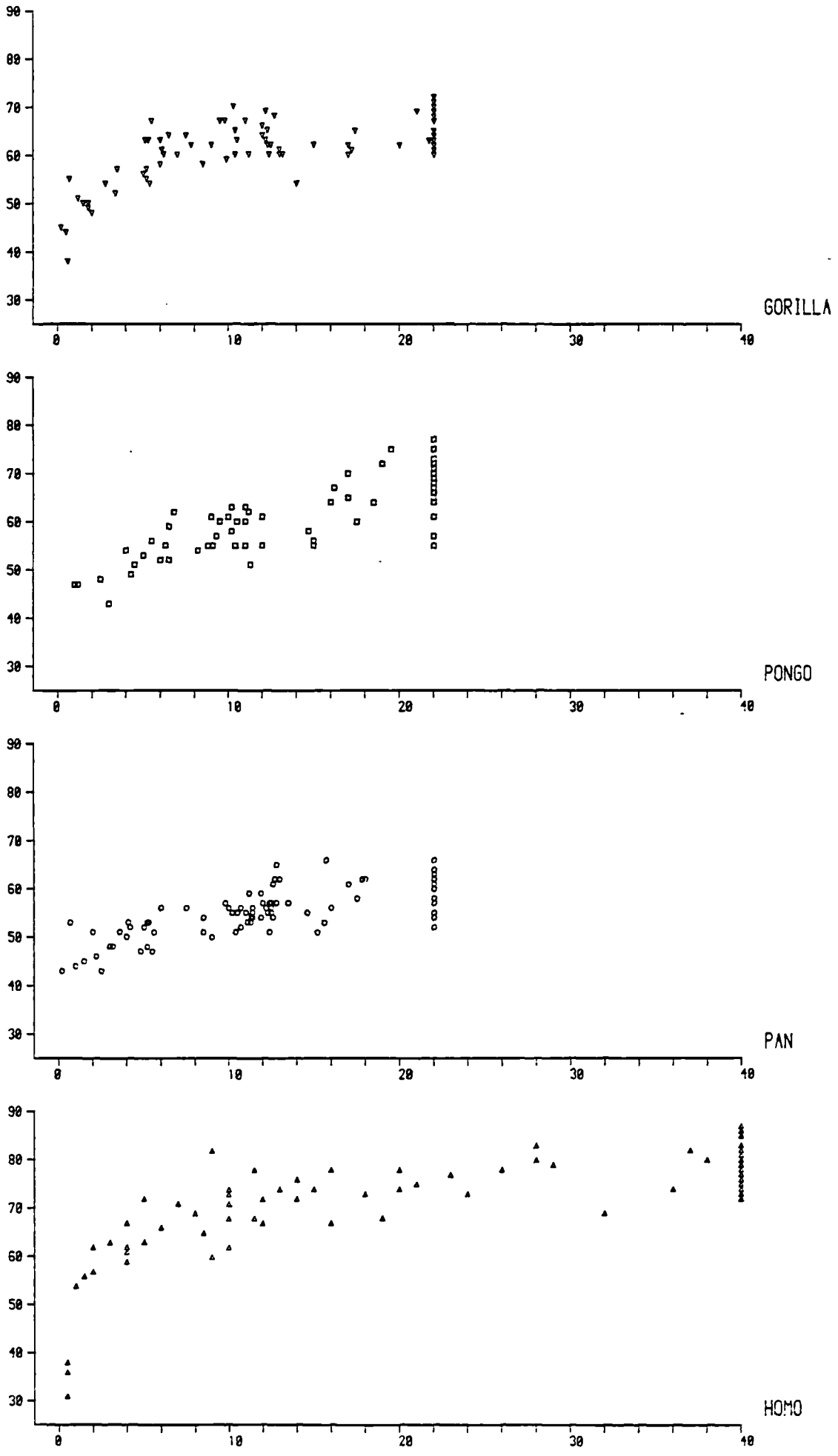
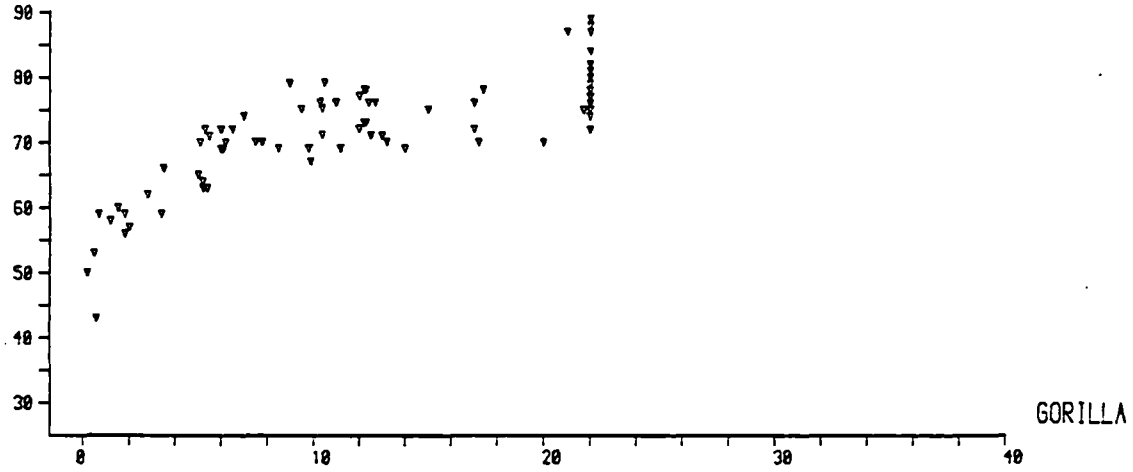
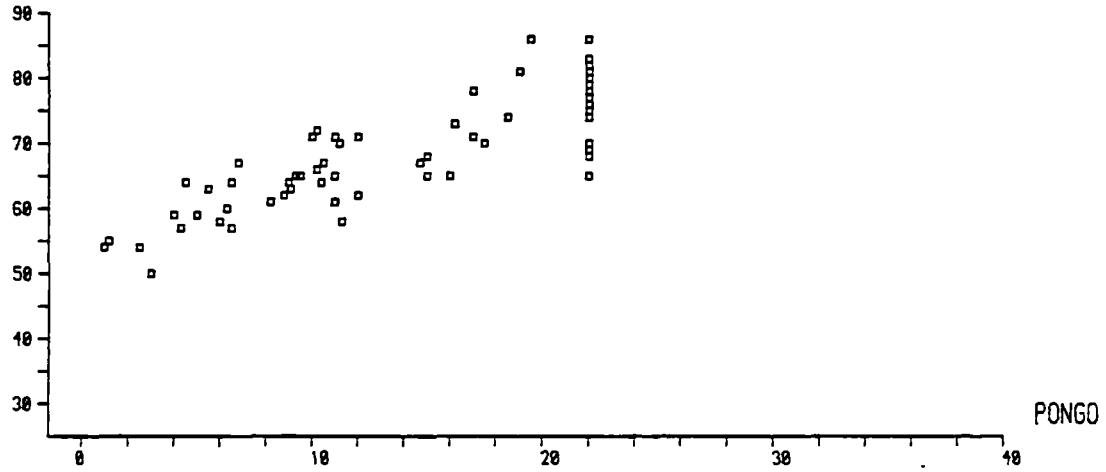
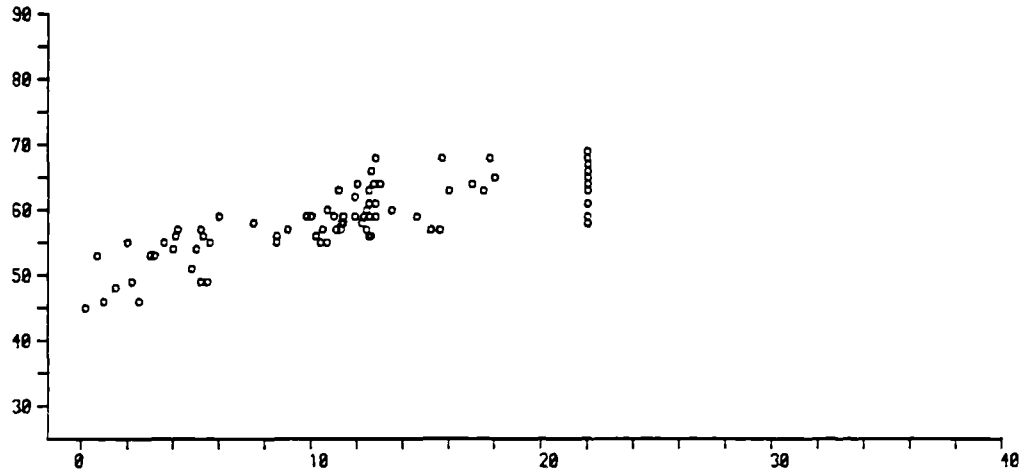
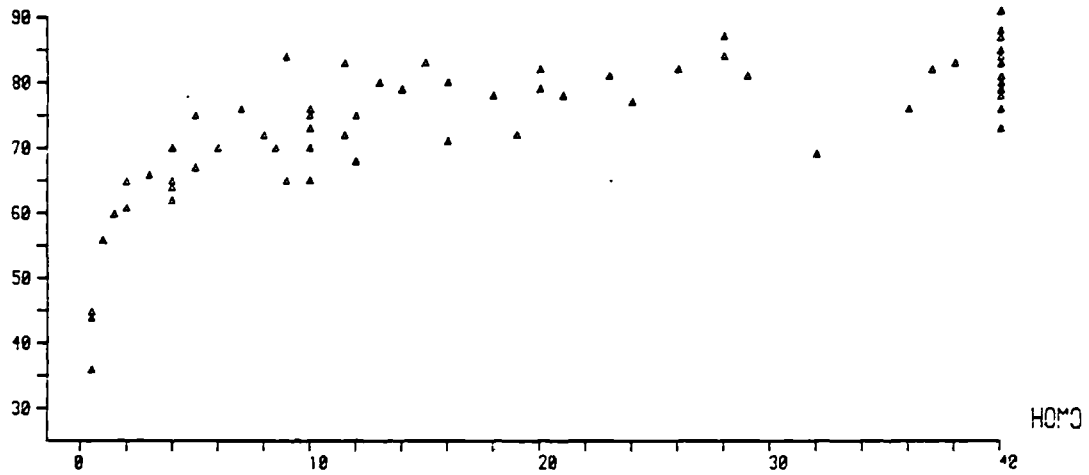


Figure 35 SM - SM









year in Pan, Pongo and Gorilla are 49, 55 and 55 respectively. These values rise to adult mean values of 64, 76 and 80.

Homo sapiens

This plot is also very similar to the preceding one for Homo sapiens. A spurt from 35 to 63 during the first year is followed by a very gradual increase to an adult mean of 82. Values within the adult range appear at about 3 years.

Measurement No. 14: Length from carotid canal to petrous apex - CC - PA, Figure 36

Pan, Pongo and Gorilla

The mean values for Pan, Pongo and Gorilla during the first postnatal year are 18, 18 and 19 respectively and rise steadily to adult mean values of 24, 28 and 30.

Homo sapiens

There is a gradual increase from a mean value of 14 during the first postnatal year to an adult mean of 19 over some 19 years. There is no marked postnatal increase in growth and very little increase in length occurs in this region throughout the growth period. This is probably due to the development of the foramen lacerum at the petrous apex.

Measurement No. 15: Length from the lateral extremity of the tympanic plate to the carotid canal - TP - CC, Figure 37

Pan, Pongo and Gorilla

The curves for this measurement closely resemble those for Measurement 8 (TP - TP) in form. The mean values for the first postnatal year in Pan, Pongo and Gorilla are 12, 19 and 15 respectively, rising to mean adult values of 32, 35 and 40. This measurement nearly triples in Pan and Gorilla but only doubles in Pongo, once more reflecting the trend apparent in Measurement 8.

Figure 36 CC - PA

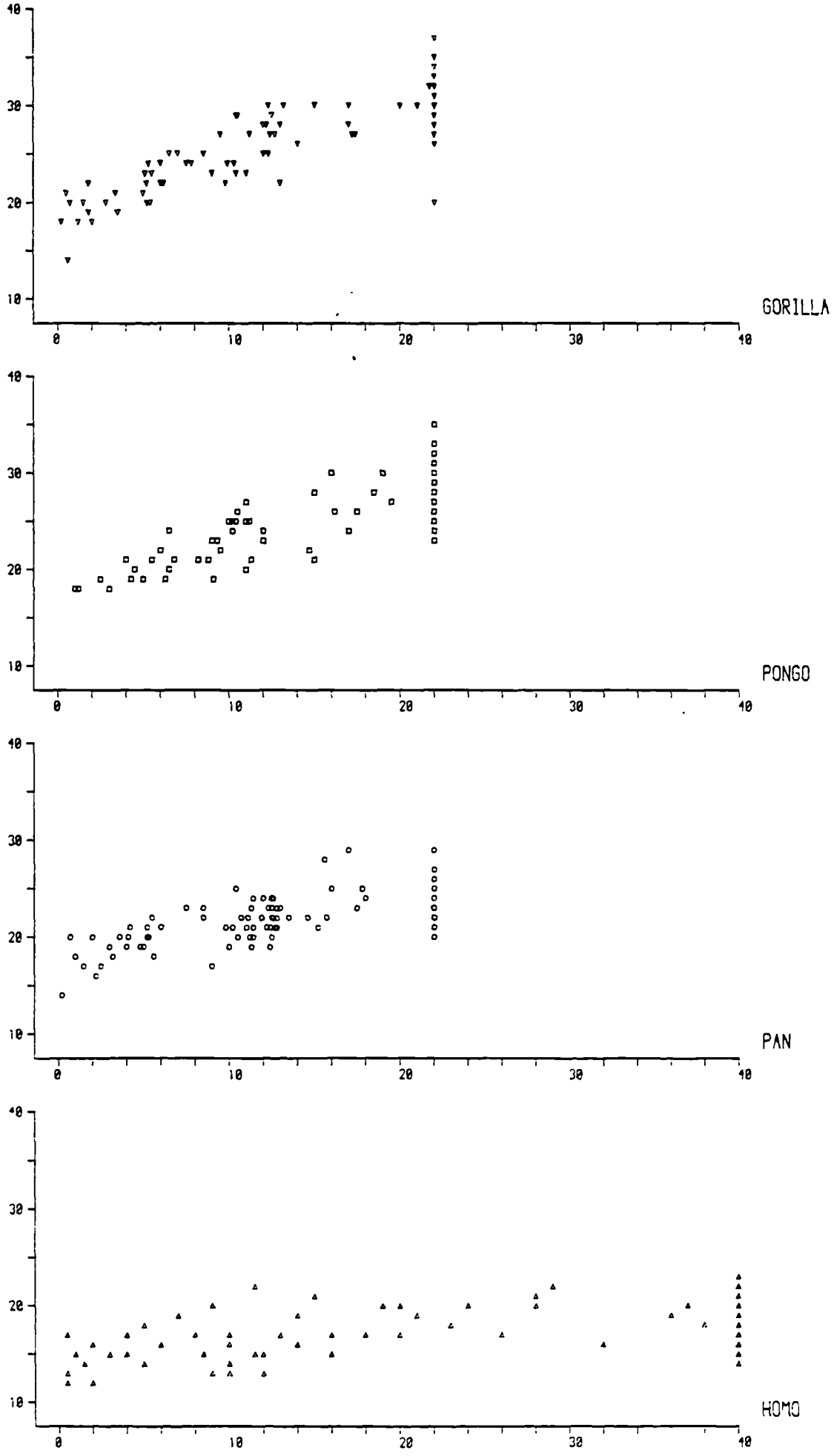
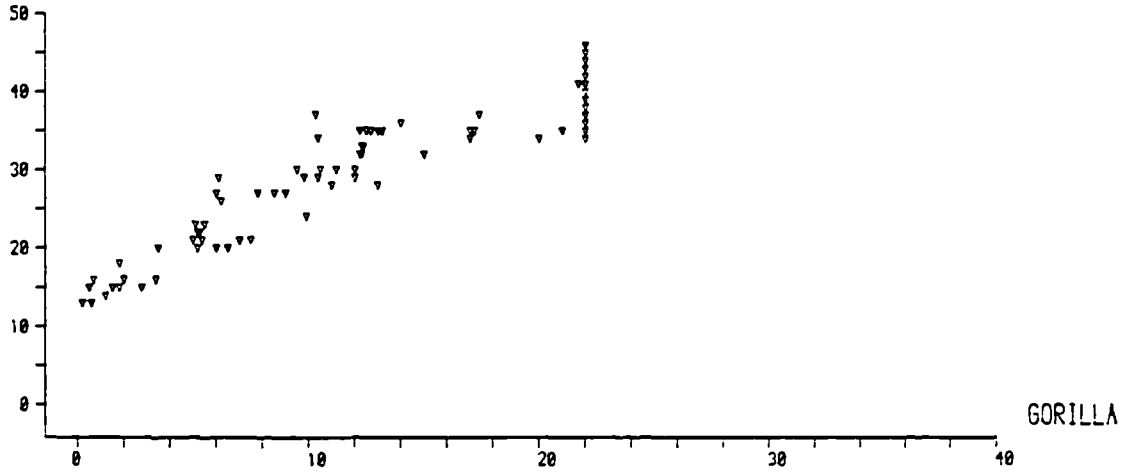
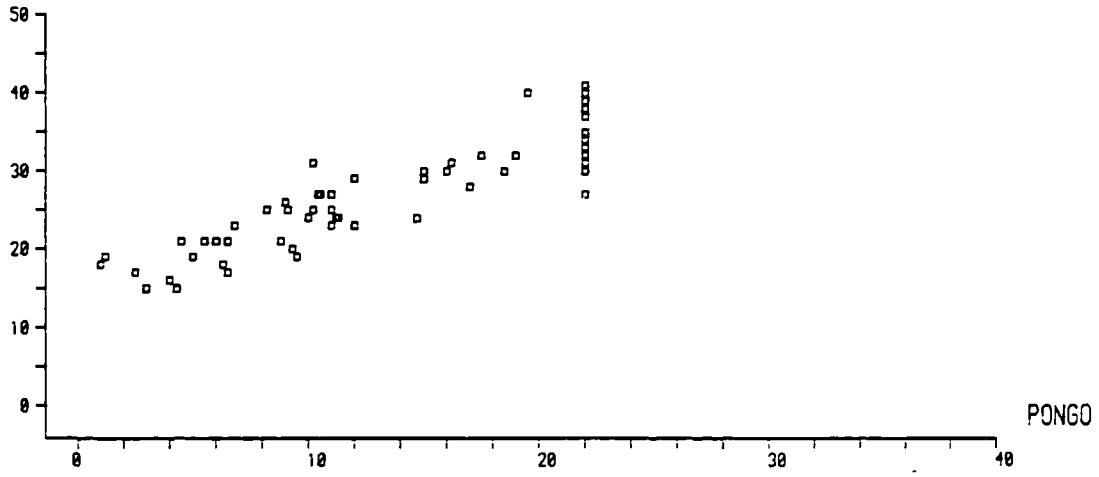
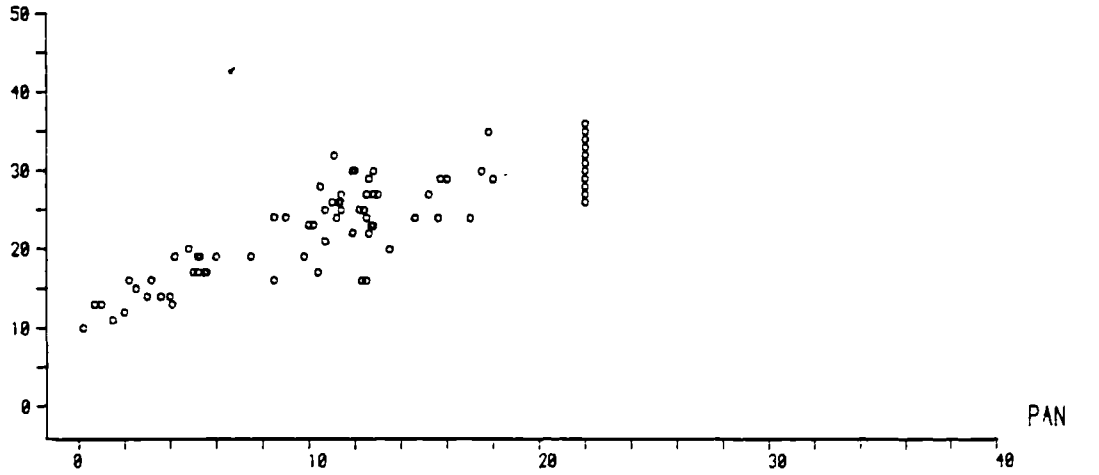
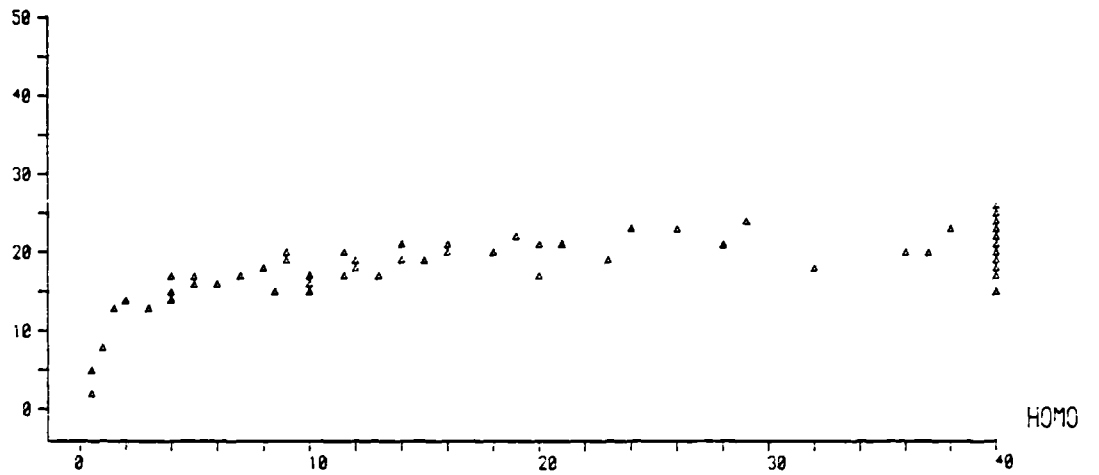


Figure 37 TP - CC









Homo sapiens

There is a spurt from about 5 to 15 during the first year, which then slowly rises over 18 years to an adult mean of 22. Measurements within the adult range are present from about 4 years of age. This growth curve also resembles that of Measurement 8.

Measurement No. 31: Angle α - CC - CC - PA, Figure 38

Pan, Pongo and Gorilla

The mean value of 58° for the first postnatal year in Pan rises to an adult mean of 69°. However, values within the adult range are present from the first year and the increase in this angle is a gradual one. The growth curve for Pan also indicates that there may be a very early postnatal decrease in this angle.

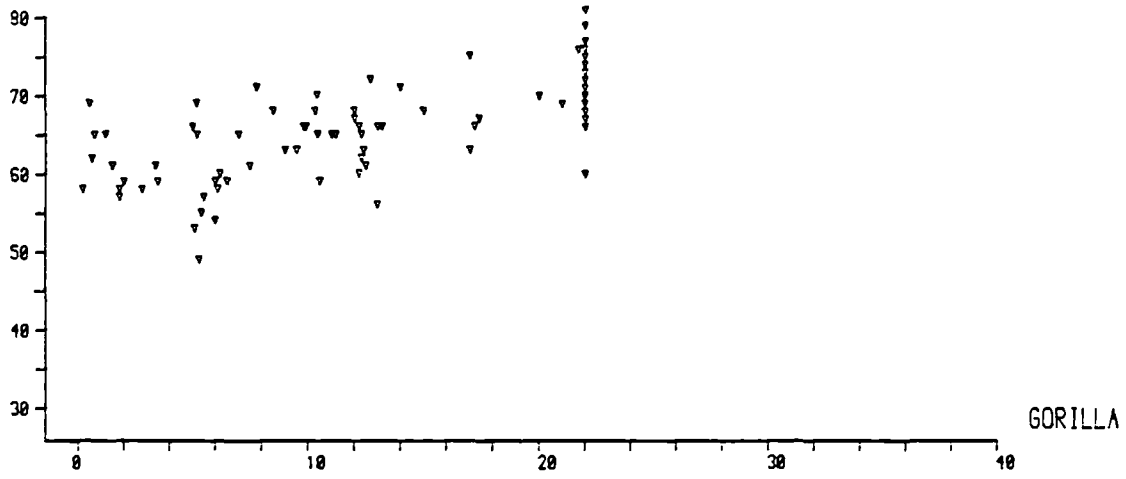
In Pongo the mean value of 59° during the first postnatal year rises gradually throughout the growth period to an adult mean value of 68°. Values within the adult range do not begin to appear until after the fourth year, in contrast to Pan and Gorilla in which they appear during the first year after birth. It is noticeable that there is less indication of an early decrease in this angle during the immediate postnatal period in Pongo.

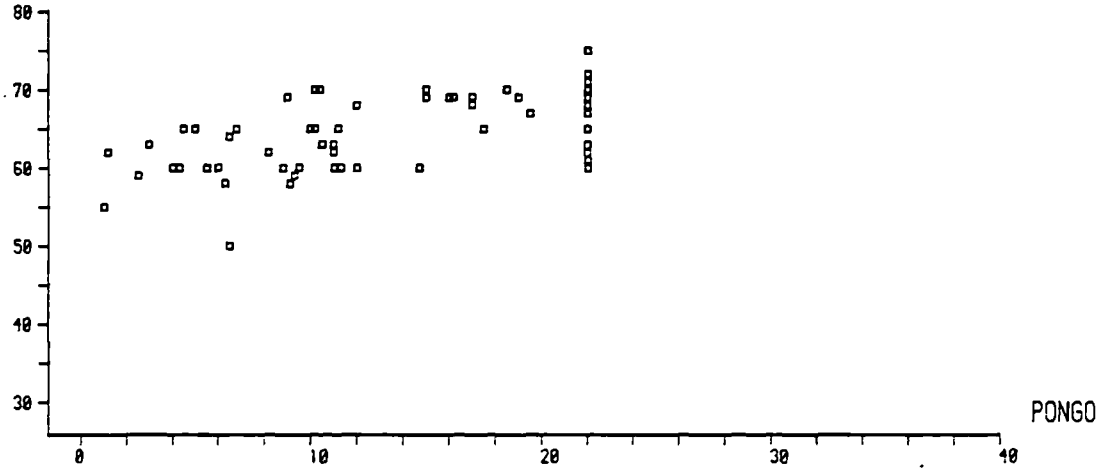
The mean value of 62° during the first postnatal year in Gorilla rises to an adult mean of 72°. Measurements well within the adult range are present from the first year and the increase in this angle is relatively small. (Like Pan, there is some indication of a very early postnatal decrease in this angle in Gorilla.)

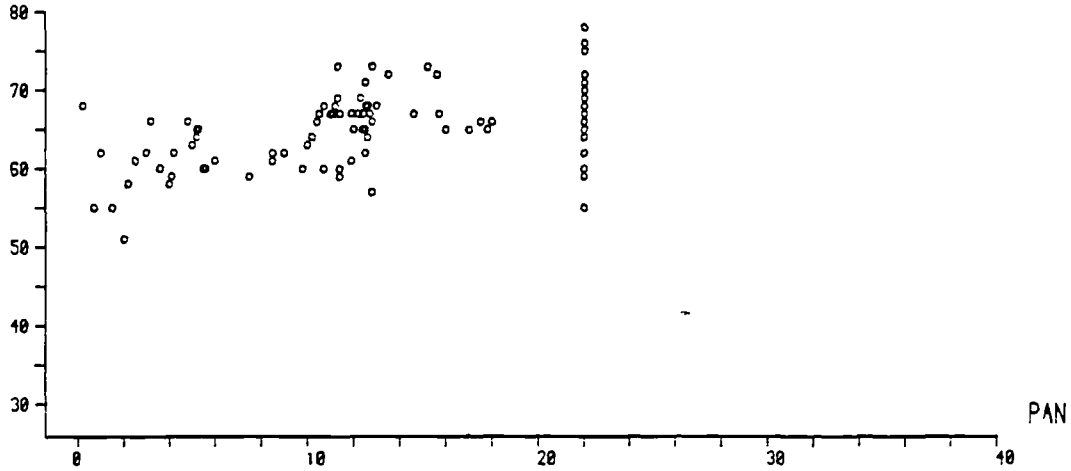
Homo sapiens

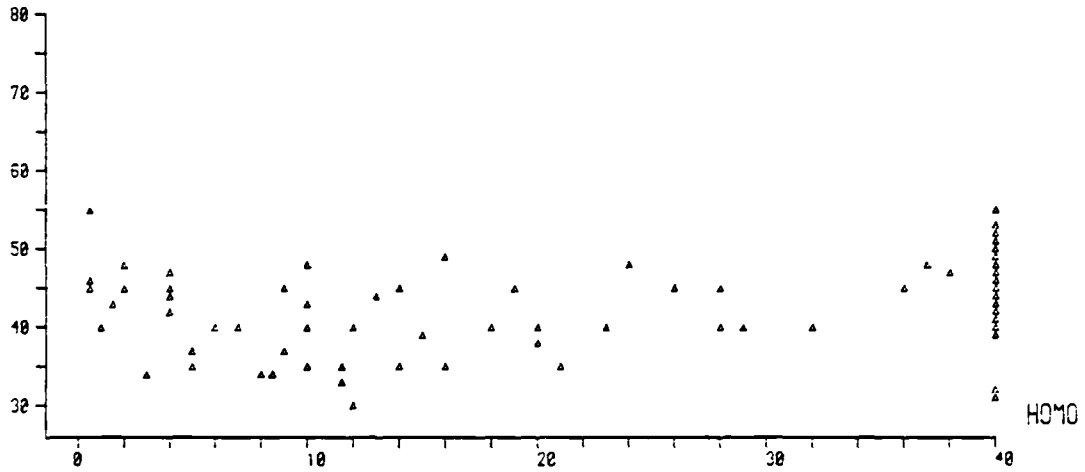
The angle α appears to fall from a mean of 46° soon after birth to a mean of about 38° at $3\frac{1}{2}$ years. After this time, there is a very slow return to an adult mean value of 46°. However, all the values from birth to adulthood fall within the adult range.

Figure 38 Angle Alpha (∝), CC - CC - PA









Measurement No. 32: Angle β - Figure 39

Pan, Pongo and Gorilla

The mean value of 84° for the first postnatal year in Pan rises to an adult mean of 96°. Values within the adult range appear at $2\frac{1}{2}$ years, after which time the increase in this angle in Pan is much more gradual than it is during the first $2\frac{1}{2}$ years.

The mean value for the first postnatal year in Pongo is 94°. This rises gradually during the growth period to an adult mean value of 101°. Values within the adult range are present from the first year and the increase in angle β in Pongo is less marked than it is in either Pan or Gorilla.

In Gorilla the mean value of 78° during the first postnatal year rises to an adult mean of 95°. Values within the adult range begin to appear at about 3 years, after which time any change in this angle is small. The increase in angle β that occurs in Gorilla is much more marked than that in Pan and Pongo.

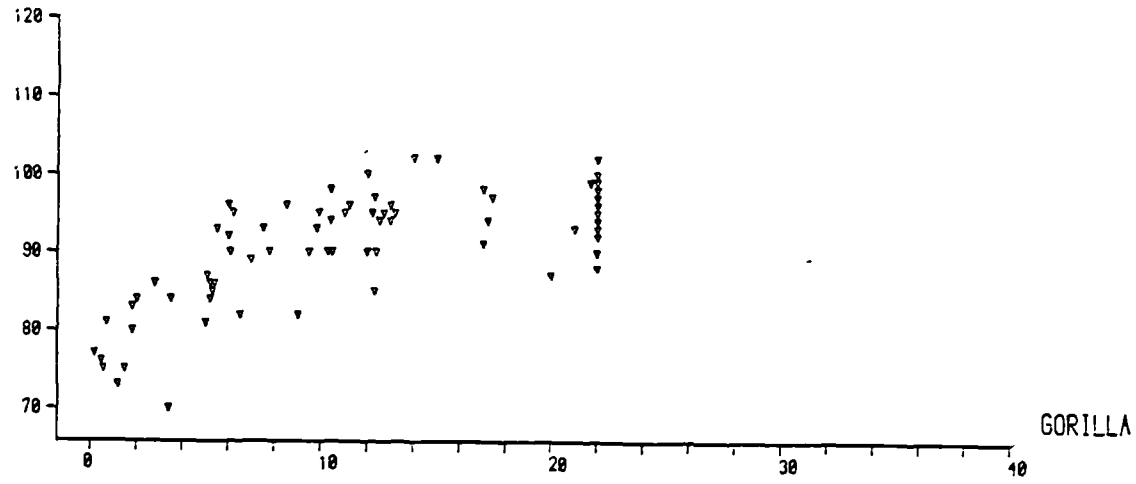
Homo sapiens

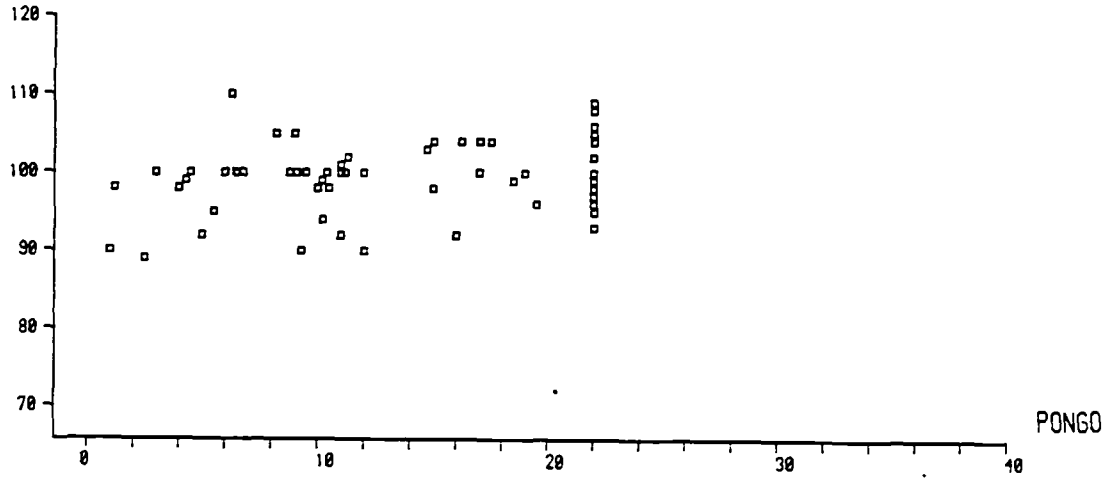
The very wide range of measurements present during the first postnatal year in Homo suggests that there might be a sudden fall from values at the top end of the adult range soon after birth to values well below the adult range within the first 3 months of birth. After this time, there is a very gradual rise to an adult mean of 107° over 19 years.

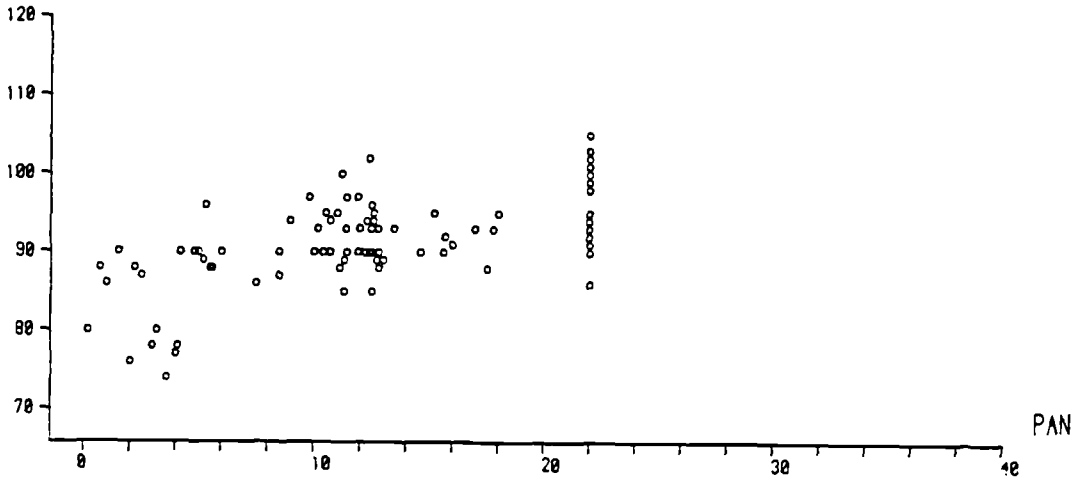
Summary of growth of the temporal bone in the three pongid taxa and Homo sapiens

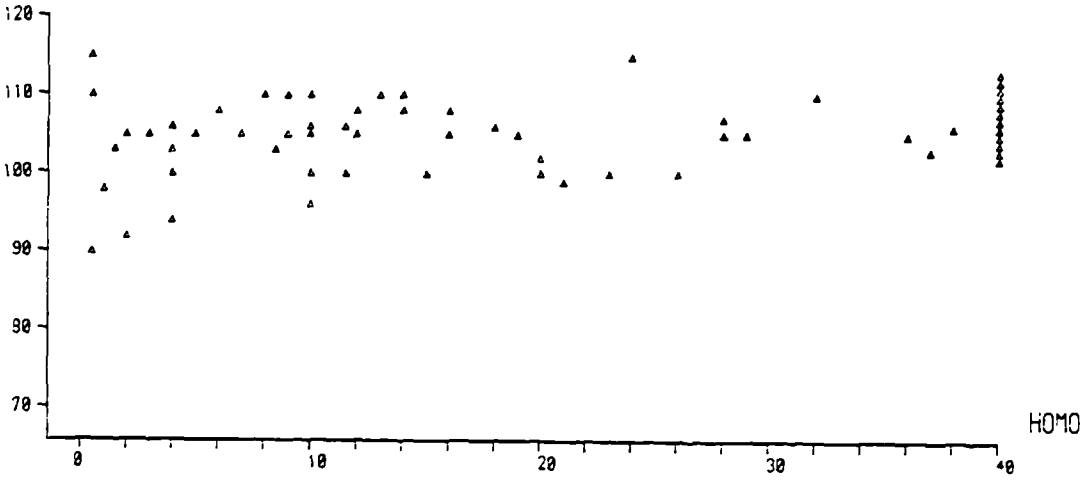
Growth in width across the bilateral structures on the temporal bones of pongids appears to fall into one of two general growth patterns. The more medial structures such as the carotid canal, petrous apex, styloid process and stylomastoid foramen,increase in width slowly. However, more

Figure 39 Angle Beta (β)









laterally placed landmarks, such as the lateral extremity of the tympanic plate, increase in width extremely rapidly. The two linear measurements show comparable increases; the more medial (CC - PA) growing at the slow rate, and the measurement incorporating the lateral landmark (TP - CC) growing at a greater rate.

The two angular measurements follow the same growth trends in all three pongids. Both angle α and angle β increase steadily throughout the growth period but the increase is small in all three taxa, and is about 10^{o} for both α and β in all the taxa (except for β in Gorilla, which increases by nearly 20^{o}).

All the measurements of the temporal bone in Homo sapiens, with the exception of the angular measurements, and the carotid canal to petrous apex measurement (CC - PA) (which appears not to increase at all), show a marked spurt during the first year after birth. This initial spurt and the prolonged growth period, even though the rate of growth during the total growth period is less than the pongid rate, accounts for the increases in width of the bilateral structures in the temporal bone seen in Homo sapiens. The styloid process and stylomastoid foramen in Homo sapiens grow at a faster rate than the more medial structures and are much more widely displaced than in the pongids. This is mostly due to the enormous spurt of the first two years. The pattern of growth of the tympanic plates is identical to this, with a tremendous spurt of 30 mm in the first year and then a very gradual rate of increase for 19 years. However, this pattern of growth still does not equal the growth in width between TP and TP which occurs in pongids, so that bi-tympanic width is reduced in Homo sapiens in comparison with the pongids. The angle α in Homo sapiens is already much less than that of the pongids during the first year after birth and then appears to decrease (at the same time the cranial base angle is reputed to increase slightly according to George (1978)). The slow increase that

follows during the growth period is only of the order of 10^{o} (i.e. similar to the amount of change in the pongids).

The angle β (again after possibly falling sharply at birth) rises from about 100^{o} to a mean of 107^{o}, once more approximately the same change of 10^{o} as occurs during the pongid growth period, but as it starts from the higher values present in Homo sapiens during the first postnatal year, it results in a higher adult mean value.

SECTION FIVE

Growth changes in the occipital bone

Three measurements only were made on the occipital bone of Pan, Pongo, Gorilla and Homo. These represent the length and width of the foramen magnum and the length of the basioccipital (Measurements 9, 10 and 13).

Measurement No. 9: Width of the foramen magnum - FM - FM, Figure 40

Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla are 20, 22 and 23 respectively. These increase very gradually to adult mean values of 23, 25 and 29, there being virtually no increase in the width of the foramen magnum after the first postnatal year.

Homo sapiens

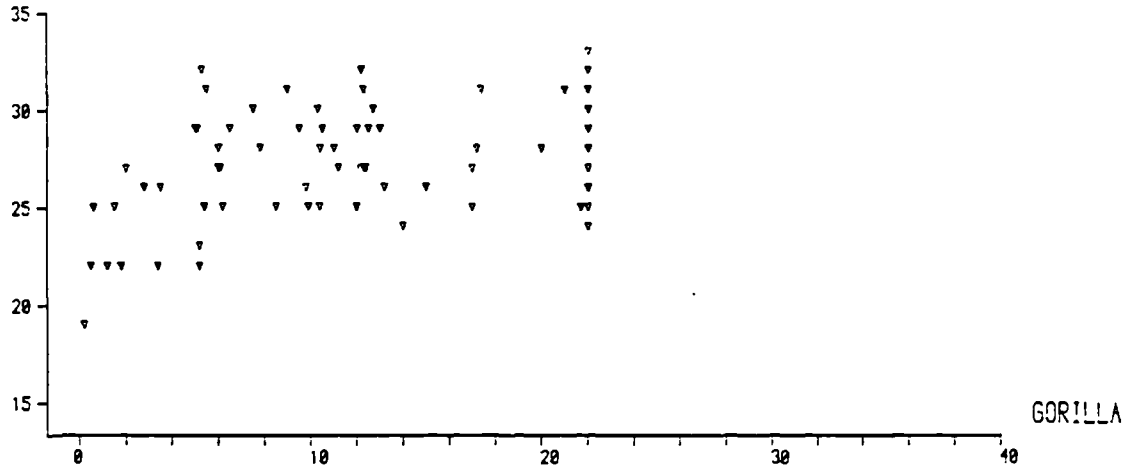
There is an increase of 10, from 15 to 25, during the first postnatal year and thereafter a very gradual increase to an adult mean of 30. Values within the adult range are present from the first year.

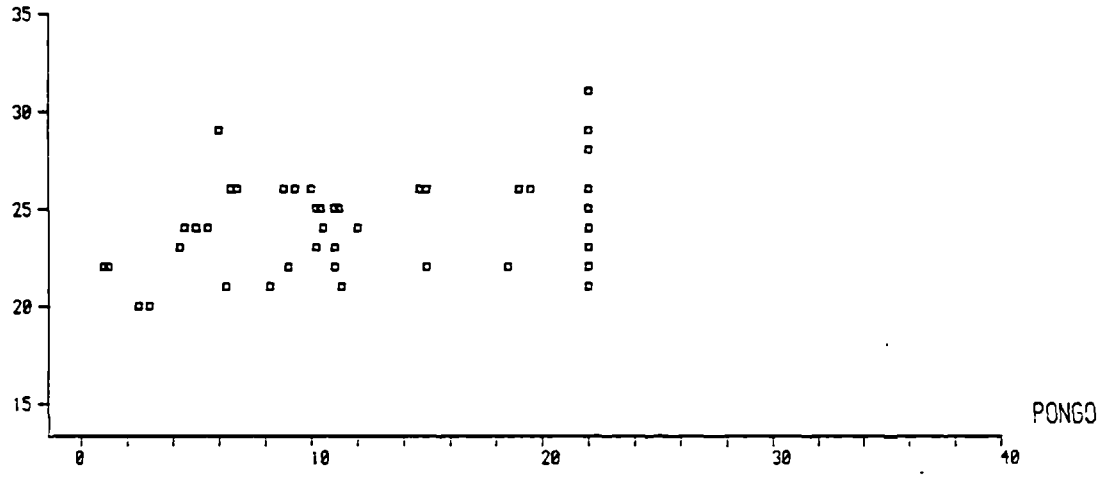
Measurement No. 10: Length of the foramen magnum - BS - OP, Figure 41

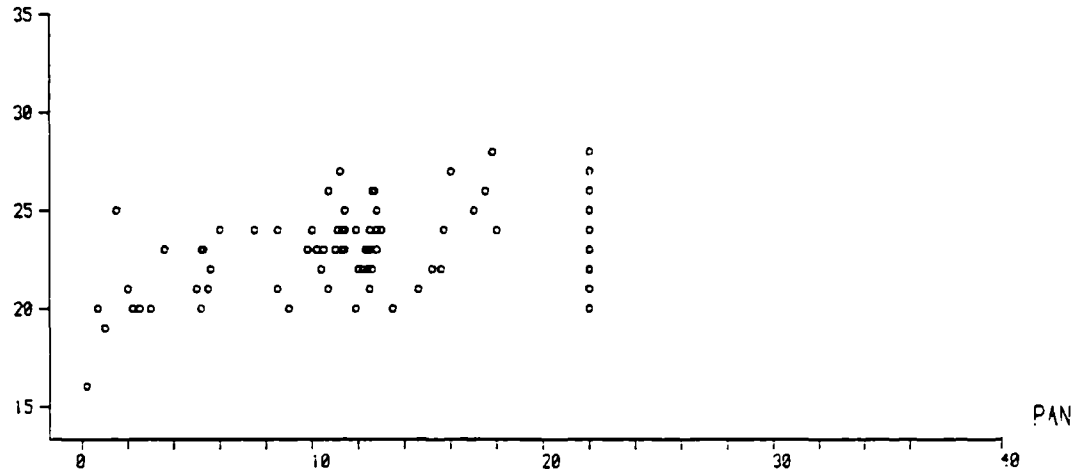
Pan, Pongo and Gorilla

The mean values for the first postnatal year in Pan, Pongo and Gorilla

Figure 40 FM - FM







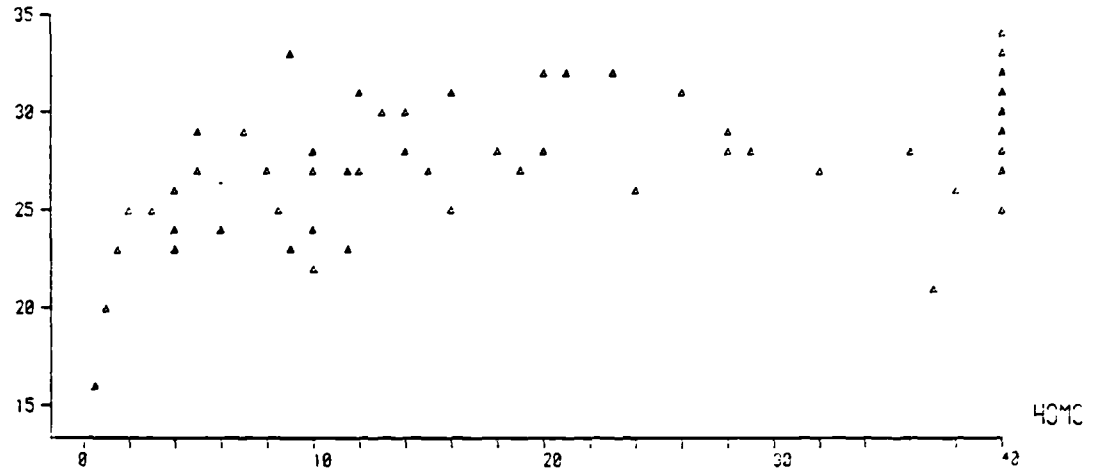
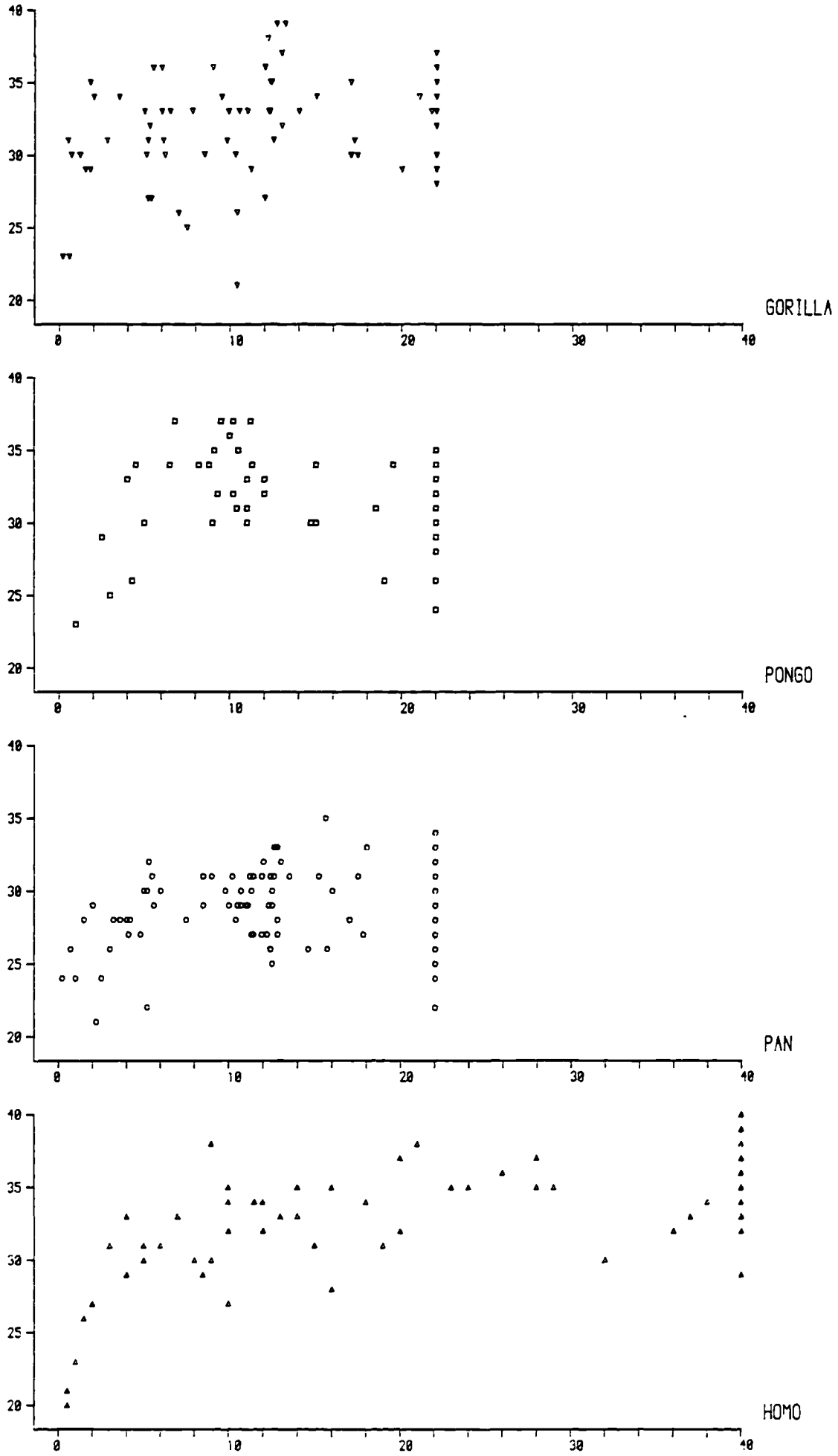


Figure 41 BS - OP



are 26, 23 and 29 respectively. These values are little different from the mean adult values of 28, 31 and 32 and demonstrate that there is little change during the total growth period. Some values for Pongo around 6 years are considerably larger than any within the adult range. These measurements were carefully checked and may indicate that a slight decrease in length of the foramen magnum can occur during growth in some specimens, or simply that the adult sample is not representative.

Homo sapiens

There is an increase from 20 to 29 during the first postnatal year and thereafter a very gradual increase to an adult mean of 35. Values within the adult range are present from the second year.

Measurement No. 13: Length of the basioccipital - BS - SB, Figure 42

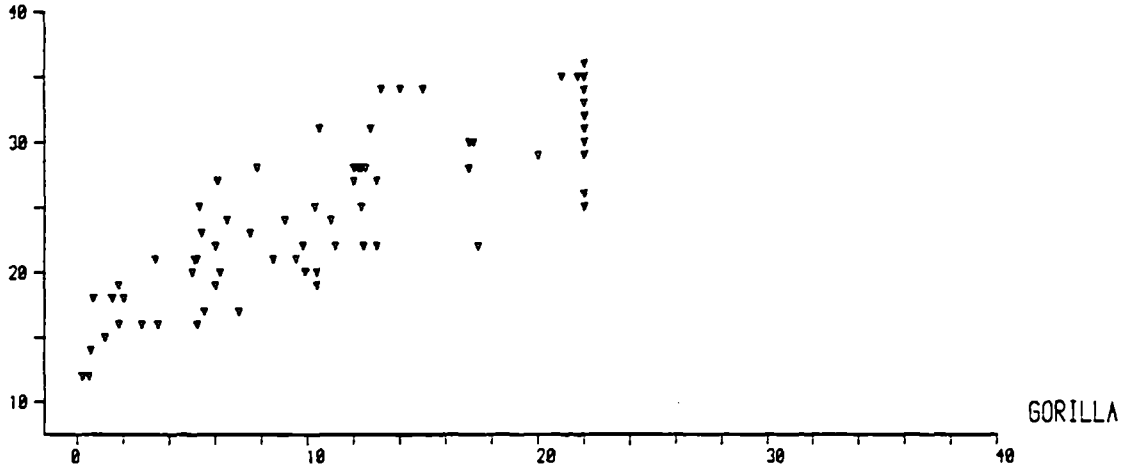
Pan, Pongo and Gorilla

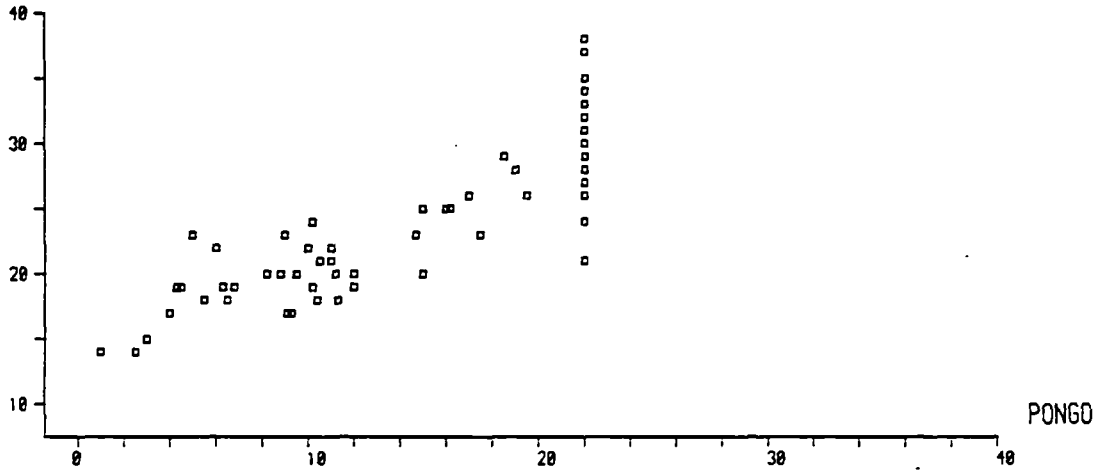
The mean values of the first postnatal year for Pan, Pongo and Gorilla are 14, 14 and 15 respectively. These rise to mean adult values of 28, 30 and 31, doubling in value in all three pongid taxa. Values within the adult range appear around 4 years in each of the three taxa.

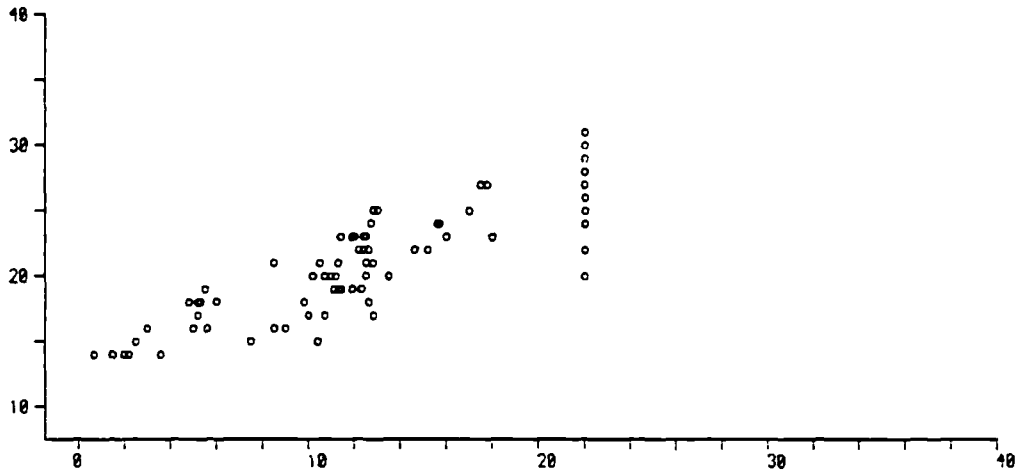
Homo sapiens

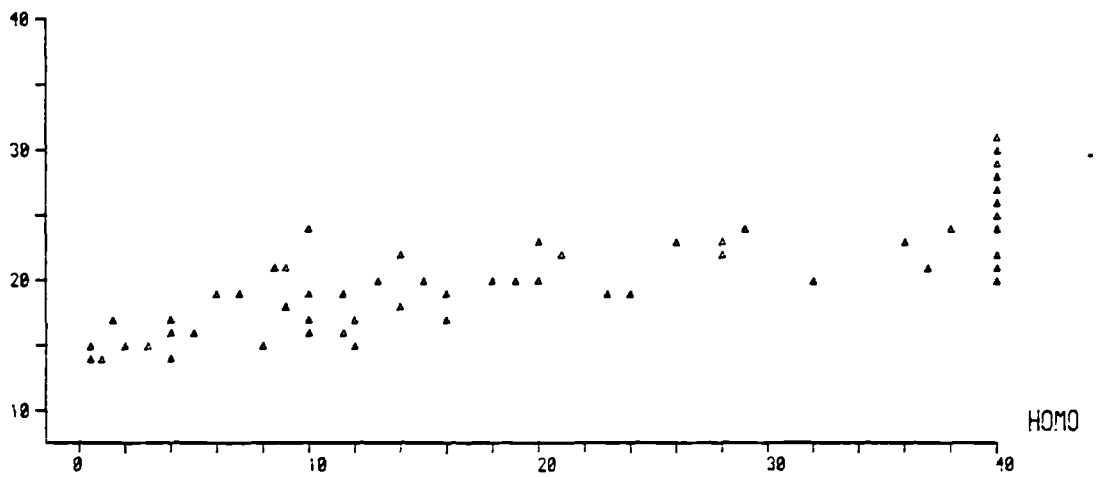
The mean value of 15 during the first year after birth in Homo increases gradually to an adult mean of 26 during the whole growth period. Like Pan, Pongo and Gorilla, the adult mean is approximately twice the infant mean and values within the adult range appear about the fifth year. There is no indication of an early postnatal spurt of growth in this measurement in Homo.

Figure 42 BS - SB









Summary of growth in the occipital bone in the three pongid taxa and Homo sapiens

The three measurements made on the occipital bone show remarkable similarities in their growth patterns in all four taxa. The foramen magnum completes growth very early and the basioccipital continues to grow throughout the whole growth period in all four taxa. The basioccipital is about the same length at birth in all the taxa but in Homo sapiens it barely reaches the pongid length, despite the prolonged growth period.

SUMMARY OF RESULTS OF GROWTH STUDY

General

Growth in the various bones of the cranial base appears to occur in a similar manner in all three pongid taxa. Differences in size apparent in the adults of each taxa appear to be due to increased rates of growth spread evenly over the whole growth period rather than to spurts of growth occurring at any one time during development. Thus a growth curve for Gorilla may show a threefold increase in the infant mean value, whereas the same growth curve for Pan may only show a twofold increase in the infant mean at adulthood. The typical growth curve for Homo sapiens is entirely different from that of the pongids and is characterised by a tremendous spurt of growth in the immediate postnatal period, followed by a steady but modest growth rate, which results in a very gradual increase in size over a much extended growth period.

Growth in width across the cranial base

Growth in width across the cranial base in the pongids is similar in all three taxa and, with the exception of bi-tympanic width, it continues at a relatively slow rate and is largely completed by the fifth or sixth year. Growth in bi-tympanic width is extremely rapid in the pongids and occurs at

a greater rate than any other (except the total length or width of the pongid skull). There is however, no indication that growth is occurring in anything but a regular, uniform manner throughout the whole growth period. The pattern in Homo sapiens is once more quite different. The overall rates of increase in width are much less for the total growth period than they are for the pongids, but most of this growth occurs in the first two years, when there is a marked spurt in growth. Growth in bi-tympanic width of the modern human cranial base is greater than the increase in width across the other bilateral landmarks in Homo sapiens and in this respect, although the growth curves are entirely different, there is a similarity between the pongid and modern human patterns.

Growth in length of the cranial base

Growth of the frontal bone in the midline occurs throughout the whole growth period in the pongids but growth in length (and width) of the cribriform plate is completed very early, at about 2 years or less. Growth of the total length of the ethmoid and sphenoid bones occurs in a different way in each of the pongids, but in all taxa it is complete by about the fifth or sixth year. Growth in the length of the foramen magnum is completed very early in the pongid taxa, but the basioccipital continues to increase in length throughout the total growth period. This general pattern of growth in length of the cranial base is very similar to that described elsewhere (and reviewed in Chapter 1) for Homo sapiens. However, the major differences are the greater amount of growth occurring in the length of the sphenoid/ethmoid complex and in the basioccipital, which occurs in the three pongid taxa.

Growth changes in angular measurements of the skull base

Three angular measurements (α, β and γ) were made on the pongid sample and two (α and β) on the sample of Homo sapiens. The cranial

base angle (γ) shows a slight increase of about 10^{o} in all three pongid taxa during the whole of the growth period. Data for Homo sapiens (reviewed in Chapter 1) indicates that there is an initial decrease of about 10^{o} in this angle during the first three years, and thereafter either a slight increase, or decrease, in this angle. The adult mean values for the pongids (between 150^{o} - 156^{o}) are about 20^{o} higher than the adult Homo sapiens mean of 131^{o} (Björk, 1955).

The results of measuring angle α indicate that there is a general increase in the sagittal orientation of the petrous bone by about 10^{o} in all three pongid taxa from about 60^{o} to 70^{o} during the growth period. In Pan and Gorilla there is some suggestion of a very early postnatal decrease in this angle.

In the Homo sapiens sample, the angle α falls markedly by about 12^{o} immediately after birth over a period of $3\frac{1}{2}$ years and then slowly rises again by some 8^{o} to reach an adult mean value of 46^{o}. In Homo sapiens a marked postnatal decrease in angle α is occurring at the same time as there is a marked decrease in angle γ , and the two changes are of roughly the same magnitude. The amount of increase in α is similar for Homo sapiens and the pongids, so that the difference in adult means is simply a reflection of the different infant mean values. The angle β in the pongid sample also increases during the growth period by about 10^{o} in Pan and Pongo (but by nearly 20^{o} in Gorilla). In Homo sapiens the value of β for the first year is higher than the pongid value, but the net increase, of some 10^{o}, which occurs during the growth period is similar in pongids and Homo sapiens.

CHAPTER 10.

Results of the dissection study of the cranial base region in Gorilla gorilla, Pan troglodytes and Pongo pygmaeus

The results of this part of the study are described in detail and are presented, together with photographs, for each of the individual specimens dissected. Only observations on the region of the cranial base are presented, and details of the more distant attachment of muscles, such as the superior constrictor and longus capitis, were not traced. The descriptions for each specimen are presented in three parts: The first part deals with the prevertebral and upper pharyngeal muscles, the second with the superficial and deep mastoid, and the third with the nuchal muscles.

Pongo pygmaeus (adult male specimen)

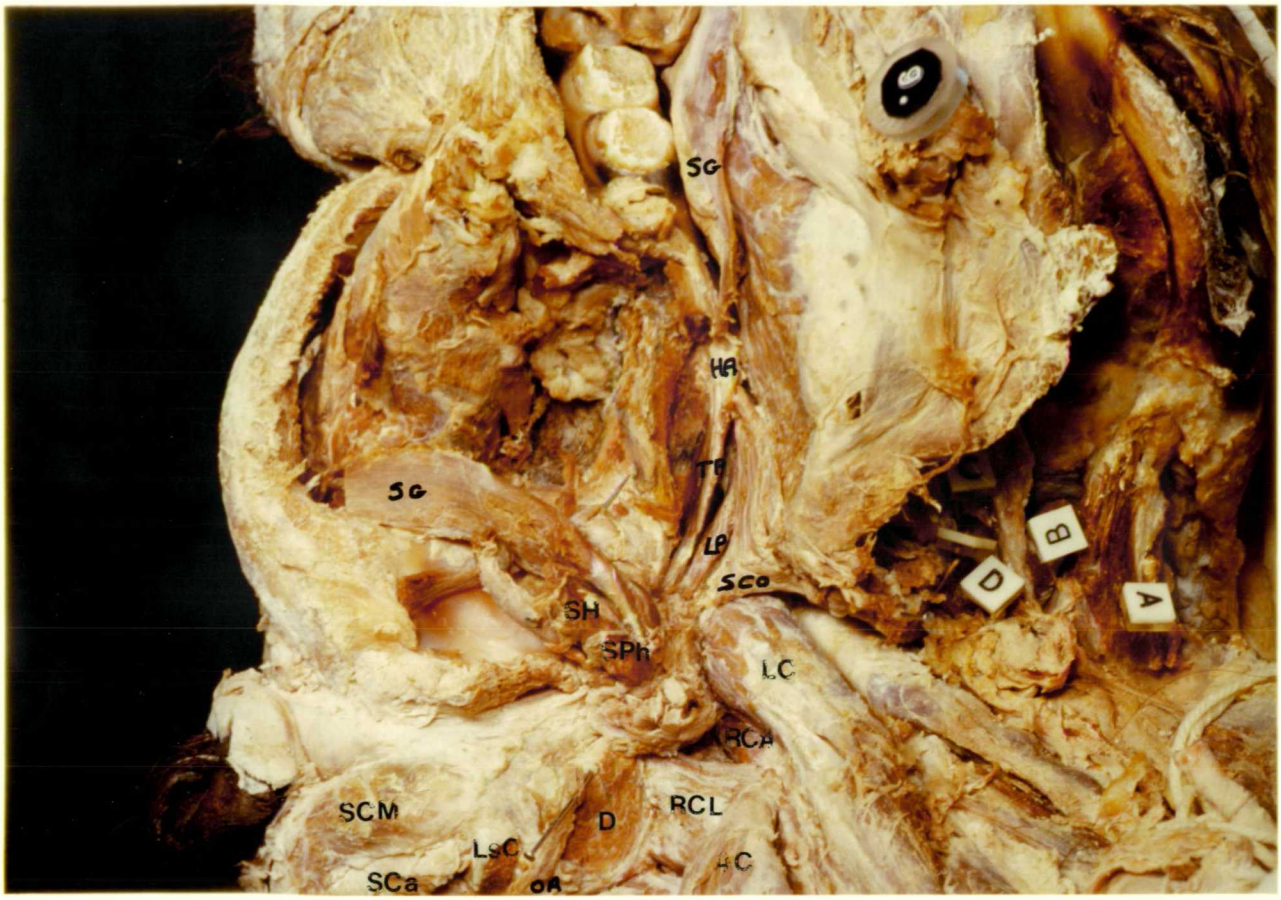
Prevertebral and upper pharyngeal muscles (Plate 3)

Rectus capitis anterior: This muscle arises from an area some 4 mm wide on the anterosuperior surface of the body of the atlas and runs towards the midline of the basioccipital, about 10 mm anterior to the foramen magnum, where it is inserted some 5 mm from the rectus capitis anterior of the opposite side. Viewed anteriorly, it is a 'fan-shaped' muscle, the base being 4 mm wide at its origin on the atlas, and the insertion some 15 mm wide on the basioccipital.

Longus capitis: This muscle is large and columnar in shape and its insertion, immediately anterior to the rectus capitis anterior on the basioccipital, is 15 mm wide and 25 mm long. The long axis of the insertion inclines slightly medially so that the anterior ends of the muscles are closer together than the rest of the muscle. The space formed posteriorly (see Plate 3), immediately anterior to the rectus capitis anterior, is filled with fibrous connective tissue which extends posteriorly between the two bellies of that muscle to the anterior border of the foramen magnum. The

List of abbreviations used to illustrate the cranial base dissections of Pongo, Pan and Gorilla (Plates 3 - 9)

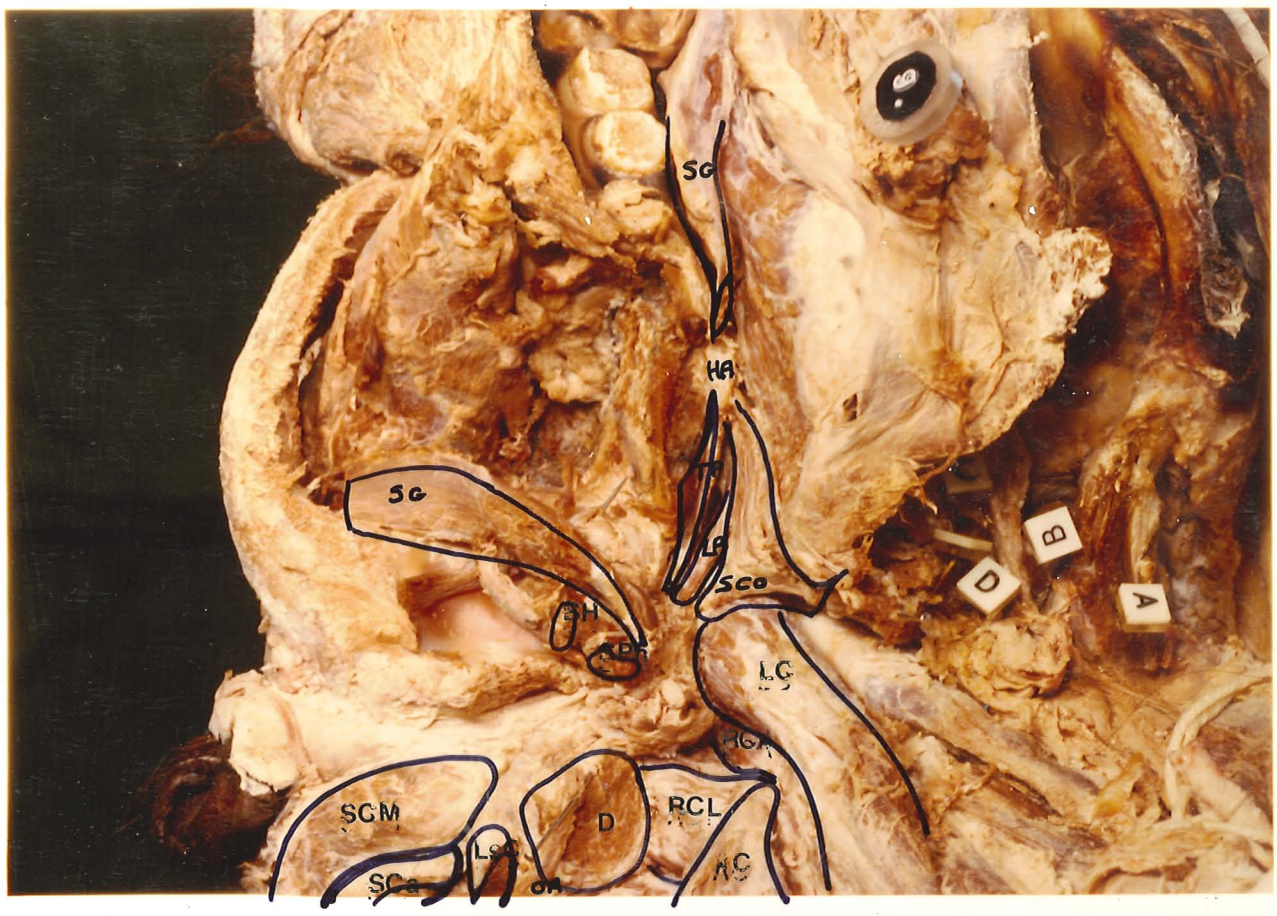
Atlantoclavicularis	AC
Biventer (semispinalis capitis)	Bi
Complexus (semispinalis capitis)	Co
Digastric	D
Eustachian process	EP
Eustachian tube	ET
Levator palati	LP
Longissimus capitis	LsC
Longus capitis	LC
Occipital artery	OA
Petrous apex	PA
Pterygoid hamulus	HA
Rectus capitis anterior	RCA
Rectus capitis lateralis	RCL
Rectus capitis posterior major	RCPMa
Rectus capitis posterior minor	RCPMi
Semispinalis capitis	SSC
Sphenoidal air sinus	SAS
Spheno-occipital synchondrosis	SOS
Splenius capitis	SCa
Sternocleidomastoid	SCM
Styloglossus	SG
Stylohyoid	SH
Styloid process	SP
Stylopharyngeus	Sph
Superior constrictor	SCo
Superior oblique	SO
Tensor palati	TP
Trapezius	T



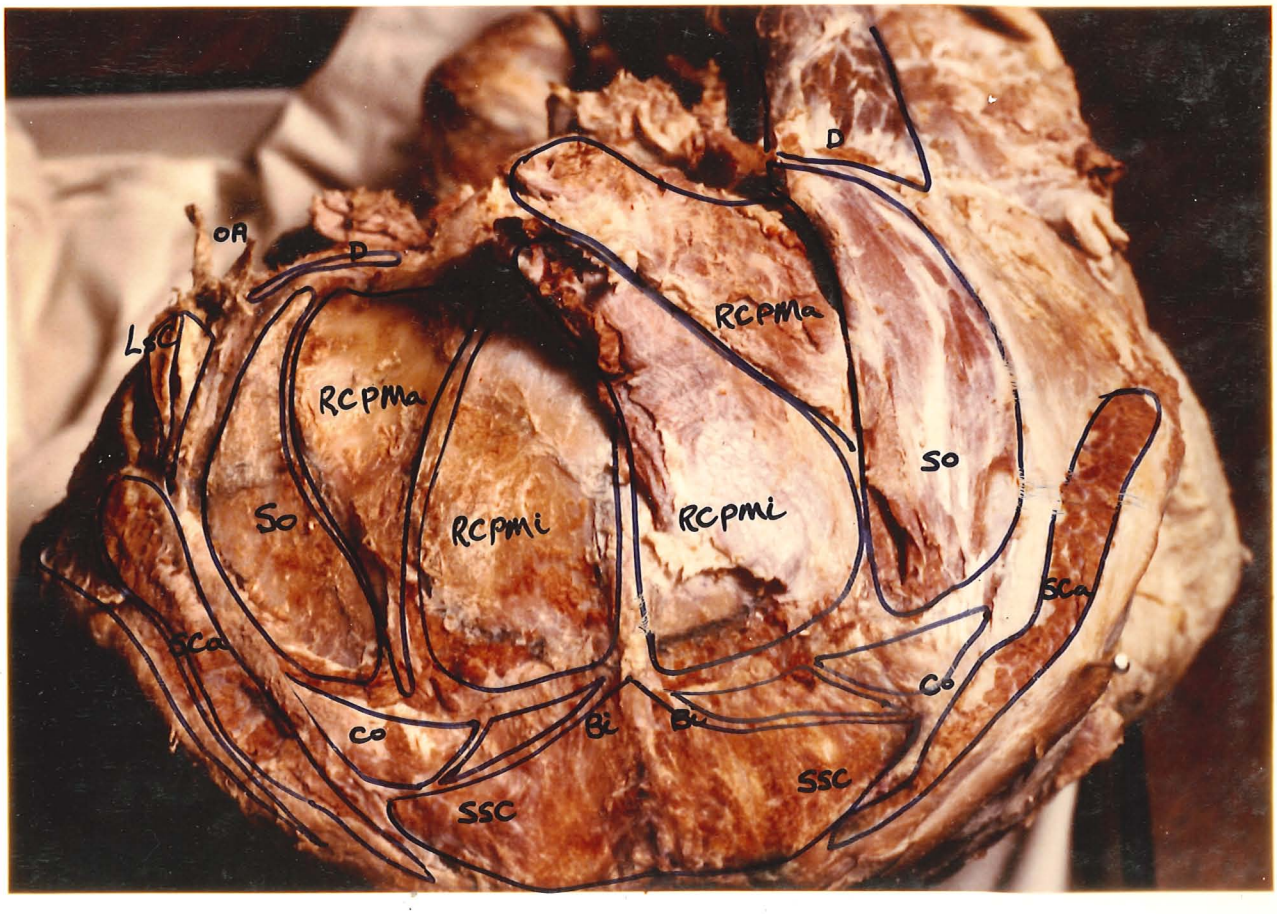
3

4

Plates 3 and 4. Plates of dissection of the cranial base region of Pongo pygmaeus.



3



4

Plates 3 and 4. Plates of dissection of the cranial base region of Pongo pygmaeus.

muscle descends for some 90 mm along the bodies of the cervical vertebrae and, at the level of the cranial base, the internal carotid artery lies on its lateral side.

Superior constrictor (see Plate 3): This muscle arises from the anterior region of the basioccipital between the grooves for the two bellies of the longus capitis and swings laterally and posteriorly around the anterior surface of the longus capitis to attach medial, and slightly posterior, to the origin of the levator palati muscle on the undersurface of the apex of the petrous temporal bone. Here, in this specimen, the nasopharynx is some 50 mm wide at the base of the skull. The fibres of the superior constrictor then run free, passing anteriorly, parallel and close to the base of the skull to be attached to the lower part of the medial pterygoid plate (see Plate 3). The pharyngobasilar facia extends from the superior border of this muscle to the base of the skull, and is 7 - 8 mm at its deepest point. The levator palati muscle passes over its superior edge about halfway along its length. From these attachments to the cranial base, the fibres of the superior constrictor pass posteriorly to blend in the midline forming the pharyngeal raphé.

Levator palati: This muscle arises immediately medial to the tensor palati muscle from the region of the petrous apex medial to the eustachian process (see Plate 3). The lateral part of the muscle is not attached to, but is in close contact with, the process and also with the tensor palati muscle (which does arise from the eustachian process). The levator palati measures some 7 - 8 mm in diameter at its origin on the petrous bone, and passes anteriorly for 55 - 60 mm, crossing the superior border of the superior constrictor to insert into the superior aspect of the soft palate over an elliptical area.

Tensor palati: The tensor palati muscle arises from the eustachian process of the petrous temporal bone and the scaphoid fossa. The superior border is horizontal and runs parallel to the base of the skull, passing immediately inferior to the cartilaginous eustachian tube (to which there is fibrous adherence but no muscular attachment) before reaching the scaphoid fossa and continuing inferiorly to the pterygoid hamulus. The distance from the eustachian process to the scaphoid fossa is 15 mm, but the pterygoid hamulus lies 30 mm in front of, and inferior to, the scaphoid fossa. The 50 mm long inferior border of the tensor palati, which passes directly from the eustachian process to the pterygoid hamulus, is particularly fibrous and this fibrous tissue is continued on the medial border of the muscle; no such fibrous sheath covers the lateral surface of the muscle.

Mastoid and deep mastoid muscles (Plate 3)

Rectus capitis lateralis (see Plate 3): This muscle lies immediately deep to the posterior belly of the digastric and measures 22 mm long by 10 mm wide at its insertion onto the jugular process of the occipital bone, where it lies lateral to the occipital condyle. The muscle is of constant diameter, and runs for 15 mm between the transverse process of the atlas and occipital bone. Cranially, it is closely related posterior to the superior oblique, medially to the capsule of the atlanto-occipital joint, to which it is firmly adherent, anteromedially to the rectus capitis anterior and laterally to the most cranial part of the posterior belly of the digastric muscle. Inferiorly, its fibres are in close association with those of the atlanto-clavicularis which arises from the inferior surface of the transverse process of the atlas (see Plate 3).

Digastric muscle: Only the posterior belly is present and it takes origin from a large area of the cranial base lateral to the rectus capitis

lateralis; its attachment measures 28 mm across and 22 mm antero-posteriorly and is not associated with any bony markings. At its origin the digastric muscle lies slightly medial, and anterior to, the superior oblique muscle (see Plate 4). The anterior half of the longissimus capitis and the most anteromedial part of the sternocleidomastoid muscles lie lateral to the digastric (see Plate 3). The occipital artery also lies lateral to the digastric muscle but does not touch the occipital bone here. It passes 20 mm behind the posterior border of the digastric muscle and comes to lie against the bone just medial to the most posterior part of the longissimus capitis muscle. The posterior belly of the digastric converges anteriorly to form a tendon measuring 10 mm by 30 mm which inserts onto the medial aspect of the posterior border of the mandibular ramus. There is no anterior belly of the digastric in the orang utan.

The styloid muscles: The styloid process lies 12 mm anterior to, and in line with the medial border of the digastric muscle at the cranial base. The process is 18 mm long and, though bony at its base, it becomes cartilaginous towards the tip. The styloglossus, stylohyoid and stylopharyngeus muscles all arise from the process, as they do in modern man (see Plate 3).

Longissimus capitis: This muscle is attached to an area of the temporal bone posterolateral to the origin of the posterior belly of the digastric muscle and medial to the most anterior part of the splenius capitis. The muscle insertion is long and thin and measures 28 mm long and 7 mm wide. In this specimen there is a small additional slip that extends forwards and medially for 20 mm, running behind the posterior border of the digastric muscle. The anterior part of the superior oblique muscle lies medial to this muscle (see Plate 4), and the most lateral part of the longissimus capitis is marked by a slight bony crest medial to the splenius capitis muscle.

Splenius capitis: This muscle inserts deep to the sternocleidomastoid and lateral to the longissimus capitis anteriorly. It continues posteriorly to within 25 mm of the midline. At its widest point it measures some 12 mm wide but its insertion tapers both anteriorly and posteriorly, where it is only 3 or 4 mm in width (see Plate 4).

Sternocleidomastoid: The mastoid insertion of this muscle begins immediately posterior to the lateral extremity of the tympanic plate and extends 45 mm medially to within 15 mm of the posterior belly of the digastric (see Plate 3). Here the muscle is widest, about 20 mm. Posteriorly, the muscle lies superficial to the splenius capitis and extends for some 100 mm, tapering to a thin fibrous insertion along the superior nuchal crest.

The nuchal and deep nuchal muscles (Plate 4)

Rectus capitis posterior minor: The cranial insertion of this muscle is fan-shaped. Its insertion on the occipital bone extends for some 50 mm posteriorly just lateral to the midline and reaches a maximum of 30 mm in width. The area of insertion of this muscle is larger than that of the rectus capitis posterior major but the muscle itself is smaller (see Plate 4).

Rectus capitis posterior major: This muscle arises as three separate heads from the spinous process of the axis. They insert lateral to the rectus capitis posterior minor on the occipital bone. The area of insertion is wider anteriorly, measuring 35 mm across, and extends to within 10 mm of the posterior margin of the occipital condyle. The insertion continues posteriorly between the superior oblique and the rectus capitis posterior minor, converging to a point about 50 mm behind the most anterior limit (see Plate 4).

Superior oblique: This muscle arises from the posterior tubercle of the transverse process of the atlas and extends for 60 mm to insert on the

occipital bone lateral to the rectus capitis posterior major. The insertion is crescent shaped and extends laterally to within 15 mm of the superior nuchal crest. It extends anteriorly almost to the posterior limit of the digastric muscle, being attached here to a bony ridge between the anterior part of the rectus capitis posterior major muscle and the posteromedial part of the digastric (see Plate 4). Posteriorly, it extends for about 65 mm, widening to a maximum width of 20 mm about halfway along its length.

Semispinalis capitis (see Plate 4): This muscle has a triangular insertion superficial to the rectus capitis posterior minor, rectus capitis posterior major and superior oblique muscles and deep to the posterior part of the splenius capitis, rhomboid and trapezius muscles. The medial biventer part extends 35 mm lateral to the midline on both sides and is 30 mm thick anteroposteriorly, where it is superficial to the rectus capitis posterior minor. No ligamentum nuchae exists and the biventer is continuous on both sides, overlying a slight midline bony elevation which becomes more pronounced towards the insertion of the rectus capitis posterior minor. Two slips make up the lateral complexus parts on each side, a deeper slip some 20 mm long and a more superficial slip some 30 mm long, both of which run laterally and parallel to the nuchal crest for about 60 mm.

Rhomboid muscle: Superficial to the semispinalis, two slips of muscle, 35 mm wide and 2 or 3 mm thick, insert just lateral to the midline. These represent the occipital insertion of the rhomboid muscles.

Trapezius muscle: This muscle rises proud of the nuchal crest superficial to all other muscles and extends round about 80 mm to join with the facia of the sternocleidomastoid.

Pan troglodytes (adult male specimen)

Prevertebral and upper pharyngeal muscles (Plate 5)

Rectus capitis anterior: This muscle is attached to the basioccipital immediately anterior to the foramen magnum and occipital condyles. It measures about 15 mm wide and 10 mm long at the bone surface and is separated from the muscle of the other side by about 5 mm. This muscle is less 'fan-shaped' than that of the orang utan and does not converge onto such a small area on the body of the atlas.

Longus capitis: The area of attachment of this muscle to the basioccipital measures 15 mm by 11 mm, the long axis lying in an anteroposterior direction. Like this muscle in the orang utan, it quickly loses its elliptical cross-section and the belly becomes circular as it descends over the vertebral bodies. The posterior surface of the upper part of the nasopharynx is marked by a groove at the junction of the two bellies of the longus capitis muscles which lie behind the superior constrictor. The space between the longus capitis muscles and rectus capitis anterior muscles posteriorly is filled with fibrous connective tissue that extends posteriorly to the foramen magnum in a similar fashion to that observed in the orang utan.

Superior constrictor: The cranial attachment of this muscle runs from a point on the basioccipital 23 mm anterior to the foramen magnum in a lateral and posterior direction, to a point immediately medial to the attachment of the levator palati on the undersurface of the petrous apex (see Plate 5). In this position, it lies 14 mm posterior to the midline basioccipital attachment. The distance between these points on the petrous apex is some 33 mm in this specimen, but internally, the superior part of the nasopharynx is only some 15 mm wide, the cartilaginous part of the eustachian tube accounting for the considerable thickening of the pharyngeal wall. The fibres of the superior constrictor run anteriorly close to, and parallel with,

the cranial base to attach to the lower part of the medial pterygoid plate. From these cranial attachments, the fibres of the superior constrictor converge to form a posterior midline raphé which runs inferiorly and posteriorly between the bellies of the longus capitis muscles.

Levator palati: This muscle arises in exactly the same way as it does in the orang utan, immediately medial to the tensor palati and eustachian process from the undersurface of the petrous apex. Superior to it (see Plate 5), the cartilaginous eustachian tube can easily be seen running forwards and medially into the upper part of the nasopharynx. The muscle measures 5 mm in diameter at its origin and passes forwards and medially to cross the superior border of the superior constrictor 15 mm along its length. The levator palati then fans out as it enters the superior surface of the soft palate.

Tensor palati: The tensor palati arises from the bony eustachian process and scaphoid fossa. The inferior border is ligamentous and resists dissection, passing for 23 mm from the eustachian process to the pterygoid hamulus before passing round and entering the soft palate. There is no fibrous muscle sheath on the medial aspect of the muscle as was noted in the orang utan. The fibres of the levator and tensor palati muscles originate in close proximity on the petrous apex, but are easily separated right down to their origin on the bone (see Plate 5).

Mastoid and deep mastoid muscles (Plate 5)

Rectus capitis lateralis: This muscle is attached to the jugular process of the occipital bone, the medial margin being 8 mm lateral to the occipital condyle. It extends posteriorly to the maximum bilateral convexity of the condyle and about halfway along its length. In the orang utan, its insertion continues posteriorly to end opposite the posterior limit of the occipital condyle, but it is situated more anteriorly in the chimpanzee. The area of

insertion is 'comma-shaped' and measures 10 mm wide by 12 mm long. Anteriorly, the area of attachment swings medially, following the curvature of the occipital condyle; at its most medial point it lies 15 mm from the midline. Posteriorly, the muscle lies close to the superior oblique muscle.

Digastric: The posterior belly of the digastric is attached to the cranial base immediately lateral to the rectus capitis lateralis, and arises from an area 9 mm wide and 17 mm long. In this specimen, the posterior origin of the digastric muscle is not associated with a groove or fossa but lies medial to the belly of the longissimus capitis, there being a slight bony elevation at this junction. It lies anterior to the superior oblique and at the most posterior part of the insertion of the digastric, a bony elevation marks the most superior part of the inferior border of the posterior belly of the muscle. Anteriorly, the area of attachment on the temporal bone turns superiorly to form part of the slope of the mastoid process. Both anterior and posterior bellies of the digastric muscle were present in this specimen.

The styloid muscles: A small ossified, but mobile, styloid process about 2 or 3 mm in length and positioned some 2 mm anteromedial to the most anterior part of the attachment for the digastric muscle, is present on both sides in this specimen (see Plate 5). This process gives rise to the stylohyoid muscle, but the stylopharyngeus, stylohyoid ligament, styloglossus and stylomandibular ligament all appear to arise from the temporal bone immediately adjacent to the pit and process. The attachments of the styloglossus and stylomandibular ligament are considerably more substantial than the stylopharyngeus and stylohyoid ligament, occupying an area of some 4 mm^2 on the temporal bone.

Longissimus capitis: This muscle attaches to the temporal bone lateral and posterolateral to the insertion of the posterior belly of the digastric. It originates some 3 or 4 mm posterior to the most anterior part of the digastric

origin and continues for 30 mm posteriorly lateral to the superior oblique, and medial to the splenius (see Plate 5). No bony markings were associated with this muscle attachment.

Splenius capitis: This muscle arises lateral to the longissimus capitis and its attachment measures about 10 mm thick maximally. It passes posteriorly to within 25 mm of the midline deep to the sternocleidomastoid and trapezius (see Plates 5 and 6).

Sternocleidomastoid: The insertion of this muscle on the mastoid process is 20 mm wide at its most anterior point, where it lies immediately posterior to the stylomastoid foramen. Posteriorly, the belly is only 7 mm in thickness. It swings laterally and posteriorly along the nuchal crest, tapering to end as a facial thickening 50 mm posteriorly (see Plates 5 and 6).

Nuchal and deep nuchal muscles (Plate 6)

Rectus capitis posterior minor: This muscle attaches to the occipital bone lateral to the midline and its insertion extends posteriorly for 40 mm. It reaches a maximum width of 18 mm and lies medial to the rectus capitis posterior major. The whole body of the muscle lies against the bone as it passes from the spine of the axis to the occipital bone.

Rectus capitis posterior major: Although the rectus capitis posterior major is a larger muscle, it partially overlies the rectus capitis posterior minor and its bony attachment is less extensive. The muscle extends further posteriorly by about 15 mm than the rectus capitis posterior minor, forming a broad marking with a pointed apex 40 mm lateral to the midline, deep to the semispinalis and superior oblique (see Plate 6).

Superior oblique: This muscle passes almost vertically upwards from its origin on the transverse process of the atlas, passing between the rectus capitis posterior major medially, and the splenius capitis and longissimus

capitis laterally. Its insertion extends posteriorly along the occipital bone for some 50 mm. Anteriorly it attaches to a fossa 15 mm wide, immediately posterior to the occipital condyles, and extends to within 15 mm of the nuchal crest, where it narrows slightly to 12 mm. Laterally it lies in a groove on the occipital bone and a prominent bony spur (see Plate 5) marks the posterolateral limit of this groove. The anterior cranial insertion contrasts with that observed in the orang utan dissected, where a raised ridge marks the anterior limit some 30 mm lateral to the foramen magnum immediately posterior to the origin of the digastric muscle. In this specimen, the superior oblique extends to within 15 mm of the lateral border of the foramen magnum and ends anteriorly in a wide area of insertion.

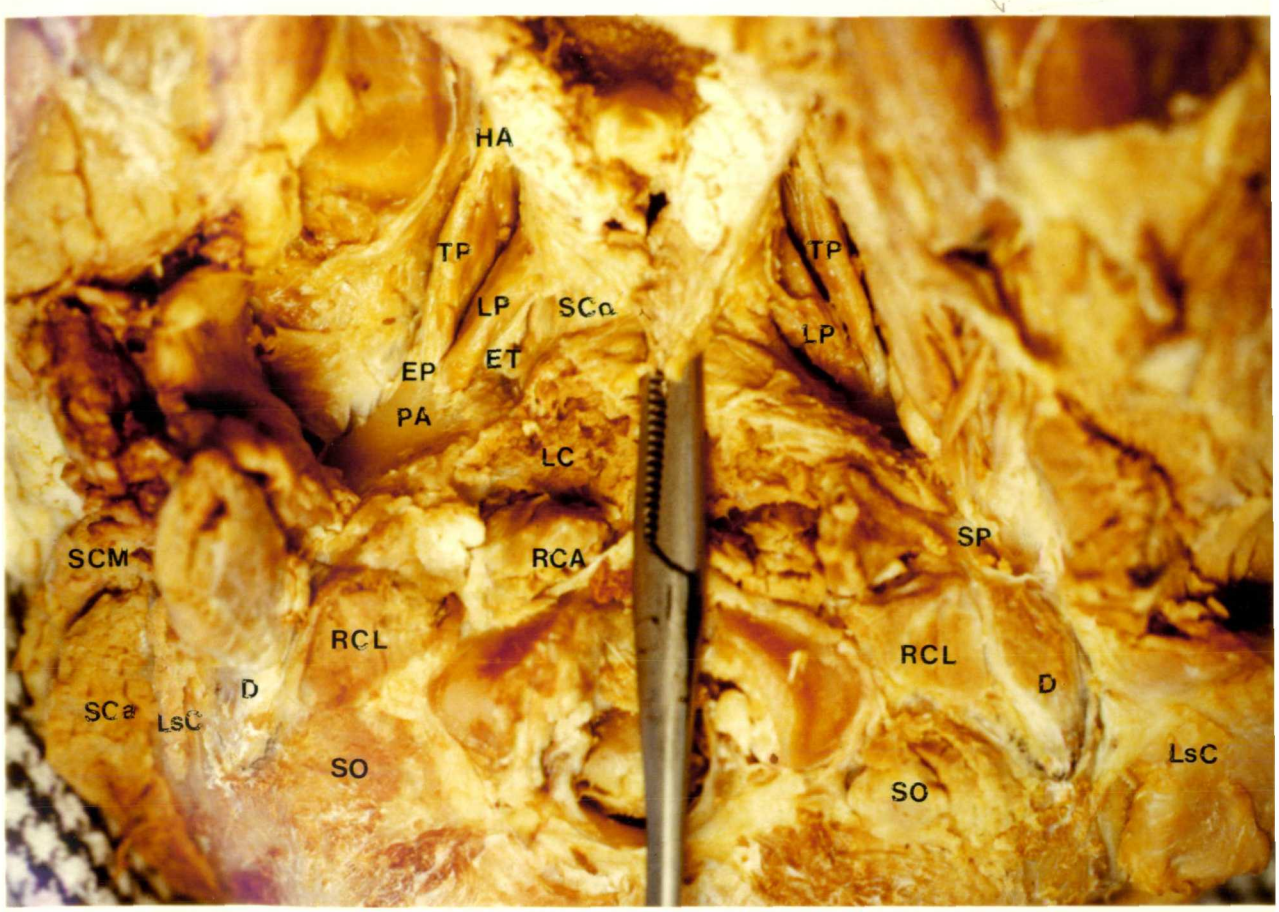
Semispinalis capitis: This muscle is less complicated than in the orang utan dissected and not as easily divided into medial biventer, and lateral complexus, parts. The muscle extends for 50 mm either side of the midline posteriorly and is partially divided by a prominent bony external occipital protuberance, although in this specimen there is no sign of a ligamentum nuchae between the two muscles. The muscle on each side leaves a deep hollowed base medially. This measures some 25 mm anteroposteriorly, but tapers laterally to a pointed apex that ends deep to the splenius and just lateral to the bony spur for the superior oblique.

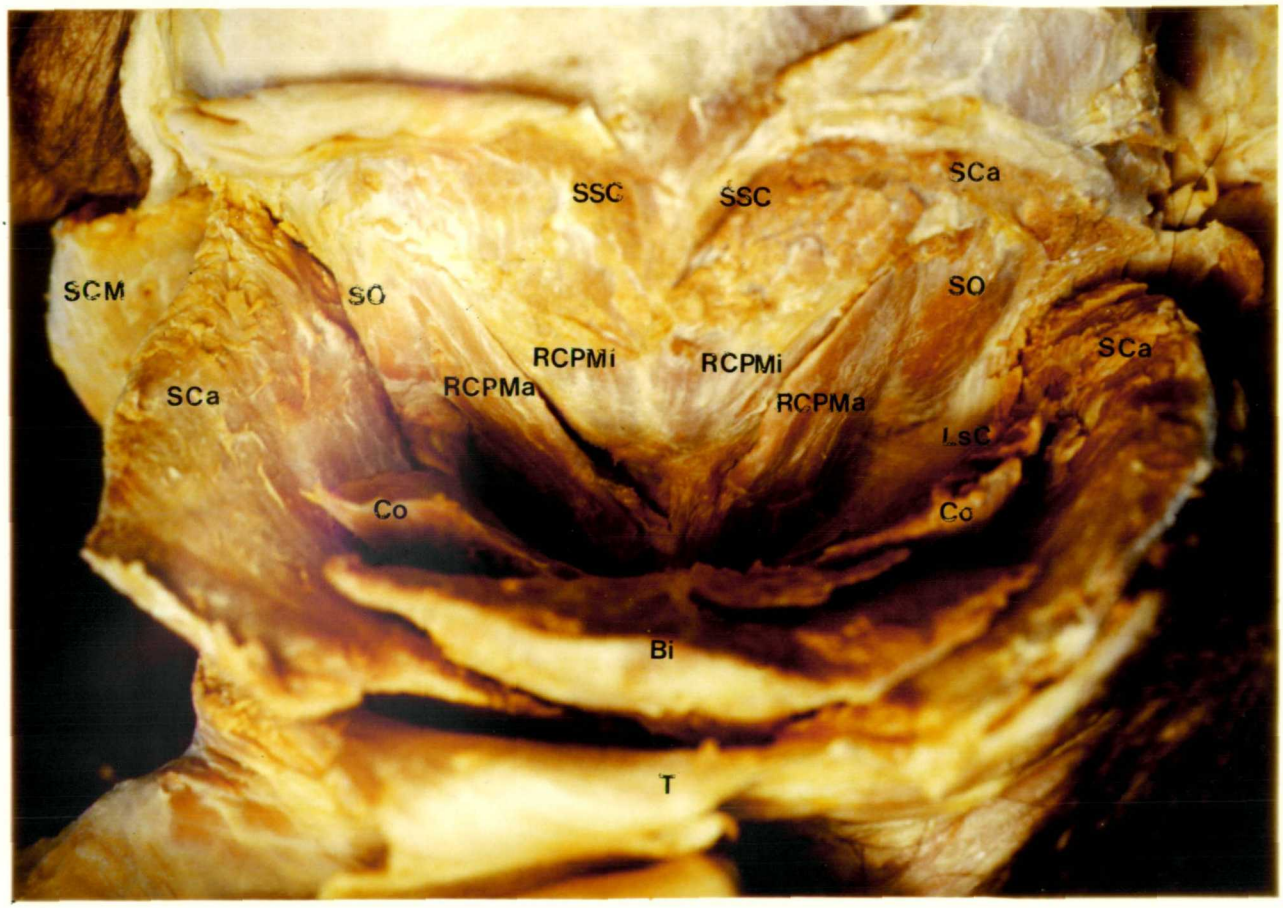
Trapezius: This muscle attaches to the nuchal crest and rises proud of it for about 50 mm either side of the midline. Its fibres run almost horizontally as it passes laterally to the scapula and clavicle.

Pan troglodytes (Juvenile specimen)

Prevertebral and upper pharyngeal muscles (Plates 7 and 8)

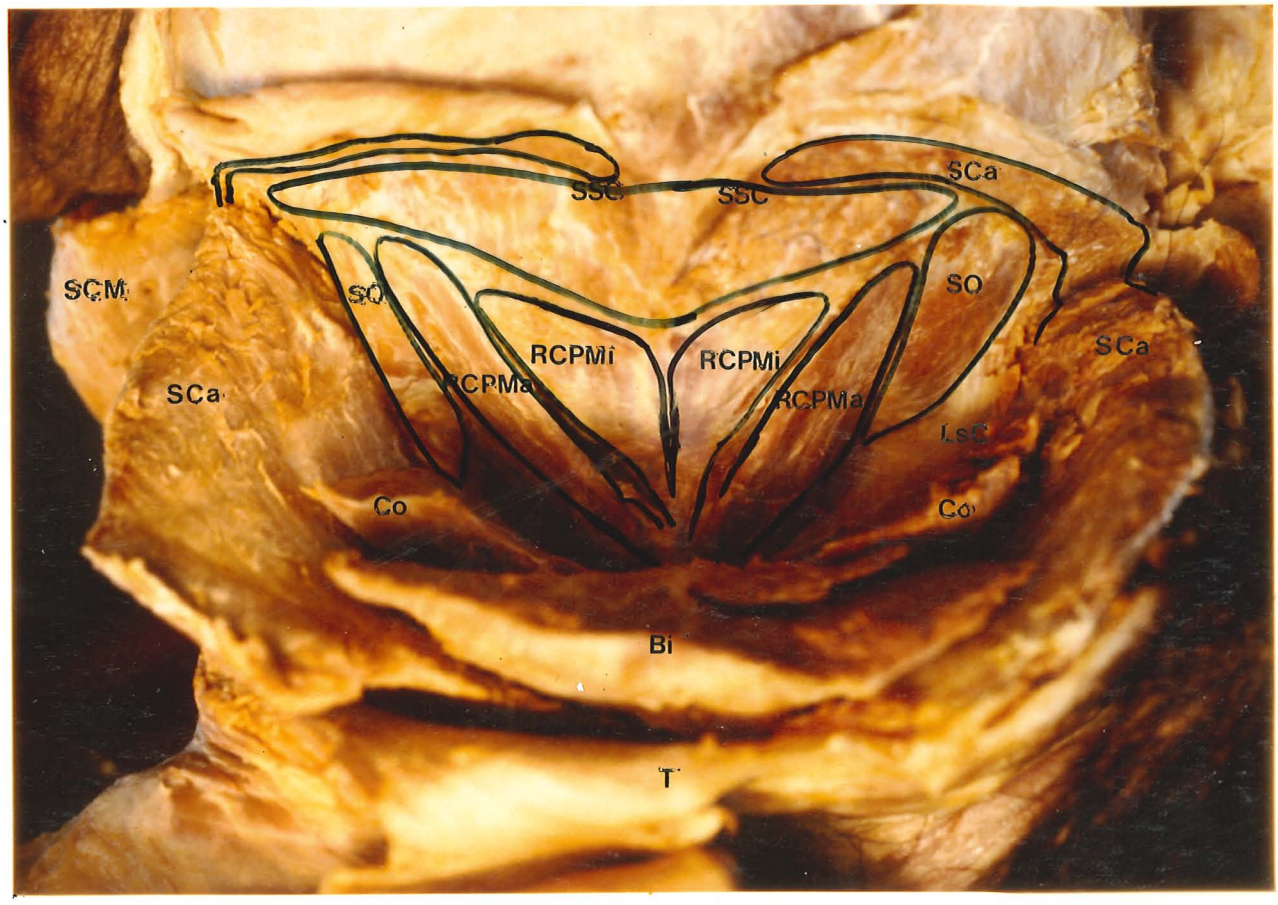
Rectus capitis anterior: This is a very small muscle in this specimen, lying posterolateral to the longus capitis. It measures some 3 mm across





Plates 5 and 6. Plates of dissection of the cranial base region of Pan troglodytes (specimen 1).

5.



6.

Plates 5 and 6. Plates of dissection of the cranial base region of Pan troglodytes (specimen 1).

at its insertion onto the basioccipital (Plate 8).

Longus capitis: This muscle occupies the whole of the basioccipital and extends anteriorly for 14 mm to within 1 mm of the spheno-occipital synchondrosis, It measures 8 mm across at its widest past.

Superior constrictor: The attachments of this muscle could not be determined in this specimen.

Levator Palati: This muscle arises from the medial aspect of the eustachian process and adjacent part of the petrous apex (see Plates 7 and 8). It measures 2 - 3 mm across at its origin and passes 18 mm anteromedially, to insert into the superior surface of the soft palate. It fans out to measure 6 mm in diameter at its insertion and lies immediately inferior to the cartilaginous eustachian tube as it passes medially.

Tensor palati: This muscle arises from the bony eustachian process and scaphoid fossa. The lower border passes medially 16 mm to hook around the pterygoid hamulus. The lower border did not resist dissection in the same way as it did in the previous two specimens. The muscle measures 8 mm from the base at the pterygoid hamulus to the scaphoid fossa.

Mastoid and deep mastoid muscles (Plate 8)

Rectus capitis lateralis: This muscle attaches to the cranial base just behind the most anterior point of the occipital condyles on the jugular process of the occipital bone. At its most anterior point, it is 8 mm in width and immediately lateral to the occipital condyle. The medial part of the muscle closely follows the lateral border of the condyle, passing posteriorly for 15 mm, the lateral border curves medially and posteriorly to bring the posterior part of the muscle to a 'comma-shaped' point (see Plate 8).

Digastric: The posterior belly of the digastric muscle arises immediately lateral to the rectus capitis lateralis, the medial border of the attachment corresponding with the occipitomastoid suture. This muscle leaves no bony marking whatsoever; the anterior border coincides with the stylo-mastoid foramen and the longissimus capitis lies lateral to it. The area of origin measures 5 mm by 8 mm on the left and 5 mm by 10 mm on the right side.

The styloid muscles: A bony process some 4 mm long was present 3 mm anteromedial to the anterior limit of the attachment of the digastric muscle. This process was mobile in the styloid pit. The individual muscles and ligaments are not identifiable, although it is clear that some gain attachment to the bone surrounding the process.

Longissimus capitis: The cranial attachment of this muscle passes lateral and posterior to the digastric muscle. Its insertion is 12 mm long but is extremely thin (1 or 2 mm), (see Plate 8). It leaves no bony marking in this specimen.

Splenius capitis: This muscle extends right around the neck posteriorly and is continuous with the muscle of the other side. It lies superficial to the semispinalis and longissimus capitis muscles and deep to the trapezius. Its maximum thickness is 3 mm and it leaves no bony marking on the occipital bone in this specimen.

Sternocleidomastoid: This muscle measures 4 mm in cross-section anteriorly at the level of the origin of the digastric muscle and inserts almost perpendicular onto the mastoid process. The bony attachment passes posteriorly for 30 mm along the superior nuchal line , where it meets with the fascia of the trapezius.

The nuchal and deep nuchal muscles

Rectus capitis posterior minor: This is a very small muscle in this specimen, which leaves no bony marking. It passes posteriorly for 15 mm on the occipital bone just lateral to the midline. At its widest point it measures 11 mm.

Rectus capitis posterior major: This muscle arises lateral to the rectus capitis posterior minor and, like that of the previous specimen of Pan troglodytes, it has a 'comma-shaped' attachment posterior to the rectus capitis lateralis (see Plate 8). The area of insertion is 15 mm across its long axis and lies deep to the semispinalis and superior oblique.

Superior oblique: This muscle has a broad anterior cranial insertion 8 mm wide immediately posterolateral to the rectus capitis lateralis. The insertion extends posteriorly for some 17 mm and leaves no bony marking in this specimen.

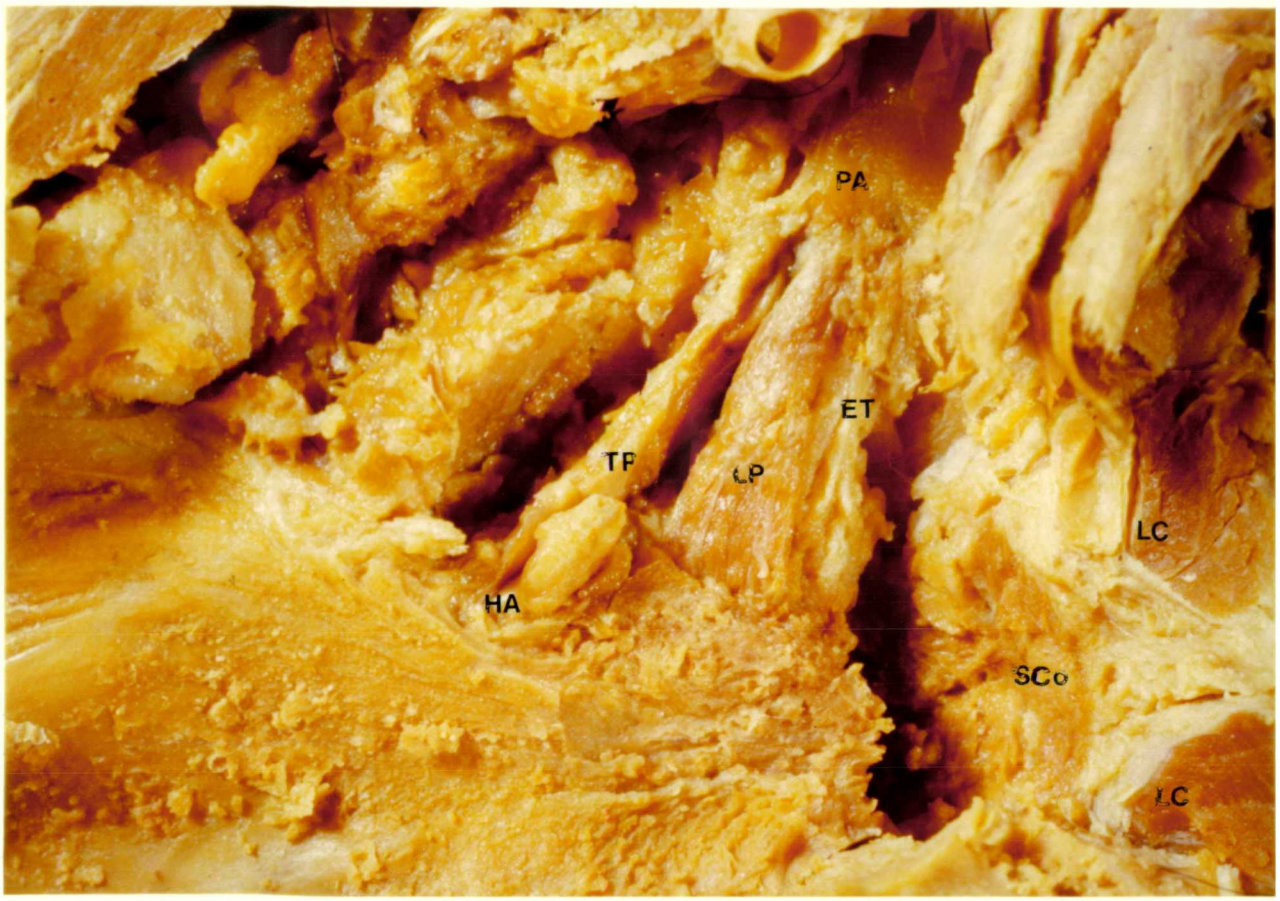
Semispinalis: This muscle is not well developed in this specimen and leaves no bony marking. Its attachment is superficial to the rectus capitis posterior minor and major, and extends for some 20 mm either side of the midline.

Gorilla gorilla (Juvenile specimen with complete deciduous dentition)

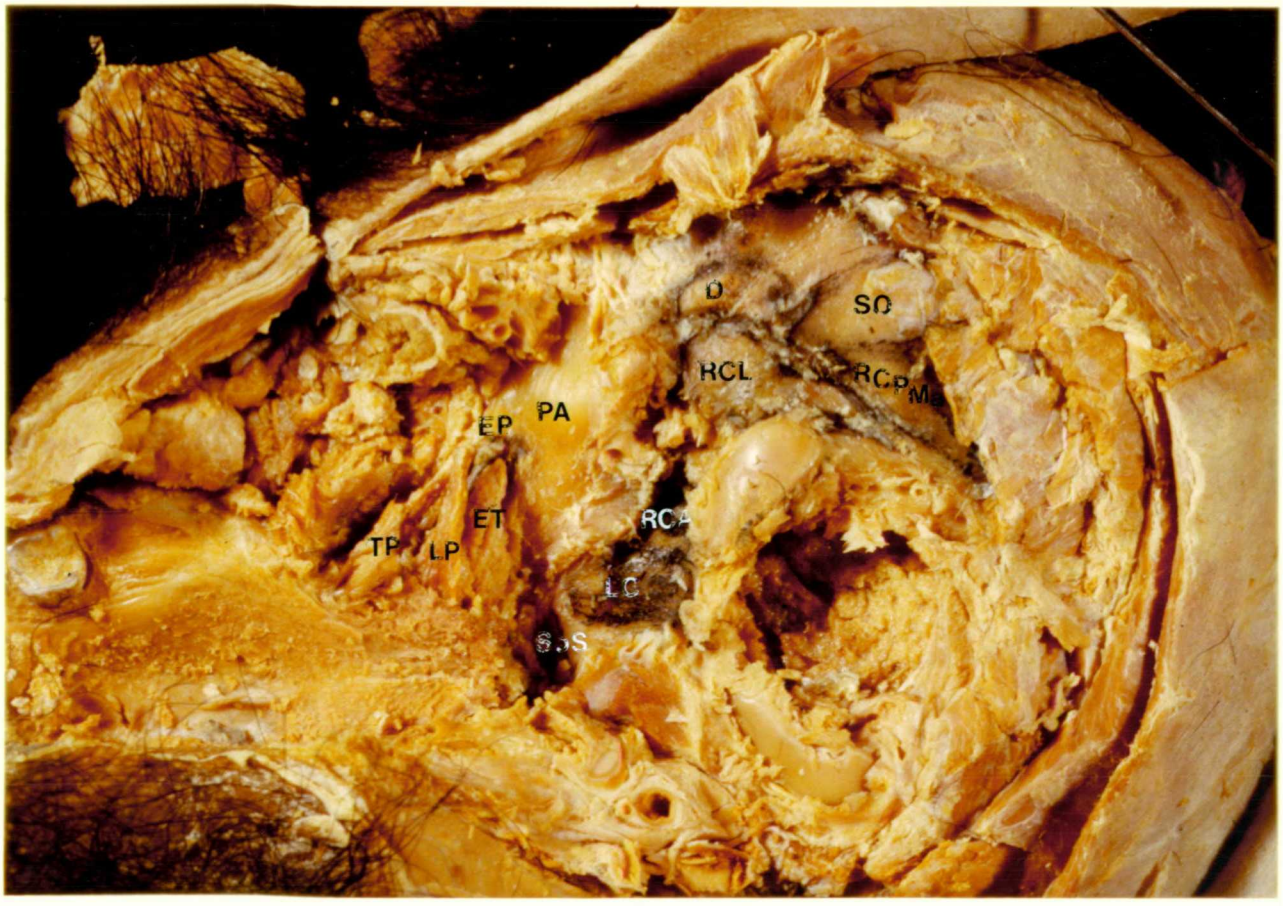
Prevertebral and upper pharyngeal muscles (There is no Plate for this very poorly preserved specimen.)

Rectus capitis anterior: It was not possible to distinguish or separate this muscle from the remains of the longus capitis in this specimen, due to the poor condition of the soft tissues.

Longus capitis: The attachment of this muscle occupied the whole of the basioccipital, extending right up to the spheno-occipital synchondrosis.

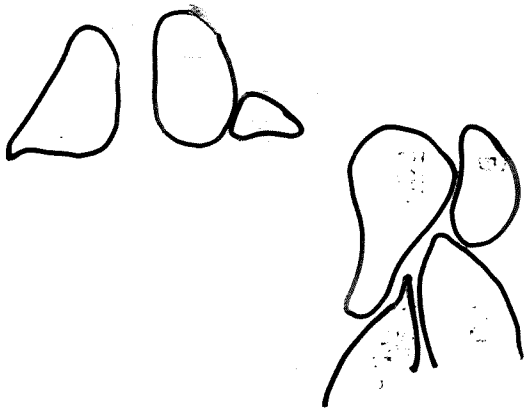


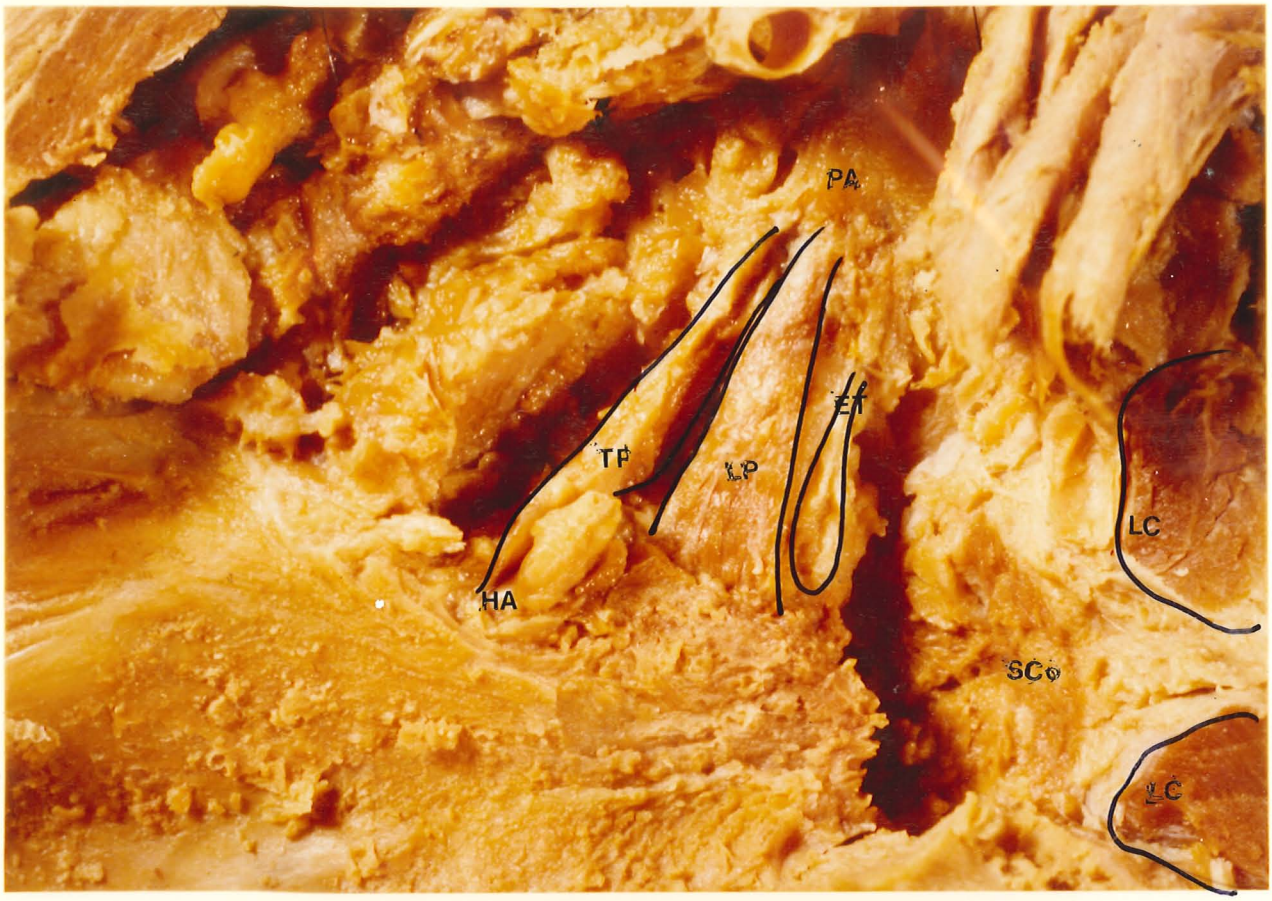
7



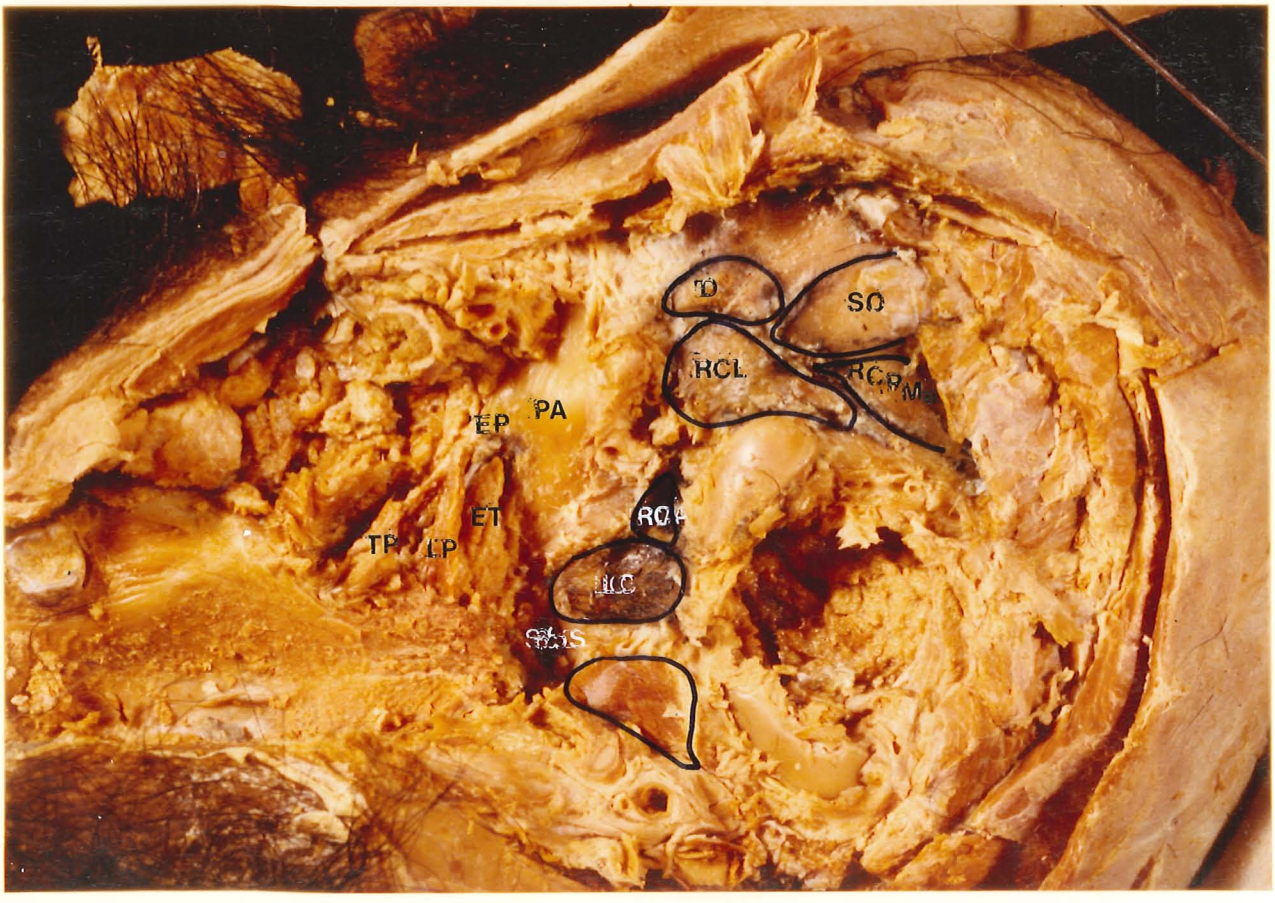
8

Plates 7 and 8. Plates of dissection of the cranial base region of Pan troglodytes (specimen 2).





7



8

Plates 7 and 8. Plates of dissection of the cranial base region of Pan troglodytes (specimen 2).

The most posterior fibres insert 7 mm in front of the anterior margin of the foramen magnum, and the long axis of the insertion continues for some 12 mm anteriorly.

Superior constrictor: As in the specimens of Pan troglodtyes and Pongo pygmaeus dissected, the superior constrictor muscle in this specimen was inserted onto the basioccipital between the two bellies of the longus capitis, the insertion continuing posterolaterally 12 mm to a position on the petrous apex immediately medial to the origin of the levator palati.

Levator palati: Only a few muscle fibres remained on the medial aspect of the eustachian process, the majority of the superior constrictor and levator palati having been previously cleaned from the specimen.

Tensor palati: This muscle arose from the tip, and undersurface, of the eustachian process, the fibres of the superior border passing anteriorly close to the skull base for some 17 mm to the scaphoid fossa. There was no marked ligamentous thickening along the inferior border of this muscle. The muscle measured 5 mm in height from the scaphoid fossa to the lower border at the pterygoid hamulus.

Mastoid and deep mastoid region

The soft tissues in this region were in such poor condition that dissection was impossible.

Nuchal and deep nuchal region

It was not possible to dissect these regions due to the poor condition of the soft tissues.

Gorilla gorilla (Juvenile ♀ specimen with complete deciduous dentition and fully erupted M_1, Plate 9)

Prevertebral and upper pharyngeal muscles

Rectus capitis anterior: It was not possible to dissect this muscle in the region of the skull base.

Longus capitis: Some remains of the cranial insertion of this muscle were present over an area measuring 22 mm by 10 mm on the basioccipital. The most posterior fibres were 5 mm in front of the anterior border of the foramen magnum and the most anterior fibres extended to the spheno-occipital synchondrosis. The two bellies of the longus capitis, although in contact anteriorly, diverged posteriorly to lie some 5 mm apart. The anterior arch of the atlas was positioned vertically above the posterior limit of this muscle and the space formed by the diverging insertions was filled with fibrous connective tissue.

Superior constrictor: The remains of this muscle curved posterolaterally around the bellies of the longus capitis for some 16 mm and. together with the mucous membrane of the pharynx, occupied an area 5 mm lateral to the longus capitis.

Levator palati: This muscle arose from the medial side of the eustachian process and petrous apex medial to the process (see Plate 9). The muscle was flattened mediolaterally, the bony attachment measuring 3 mm by 8 mm. The muscle passed anteriorly for 22 mm immediately inferior and adjacent to the cartilaginous eustachian tube, running over the superior border of the superior constrictor and entering the soft palate. The cartilaginous eustachian tube opened into the pharynx 20 mm anterior to the base of the eustachian process.

Plate 9. Plate of dissection of the cranial base region of Gorilla gorilla (specimen 2).

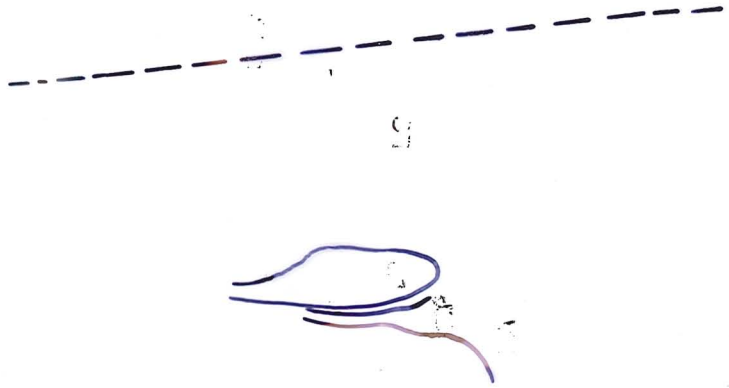


Plate 9. Plate of dissection of the cranial base region of Gorilla gorilla (specimen 2).

Tensor palati: This muscle is attached to the tip and undersurface of the eustachian process and scaphoid fossa. The medial aspect of the muscle sheath was ligamentous and resisted dissection, there being a tough broad fibrous band 6 mm supero-inferiorly passing from skull base and superior part of the process to the pterygoid hamulus. A further thickening of the fibrous muscle sheath less than 1 mm in diameter runs along the inferior surface of the process to continue along the inferior border of the tensor palati in this specimen. The muscle measured 20 mm from the tip of the eustachian process to the pterygoid hamulus and the distance between its attachments to the scaphoid fossa and the hamulus was 10 mm.

Mastoid and deep mastoid region

Rectus capitis lateralis: This muscle attaches to the skull base immediately posterior to the jugular canal and lateral to the occipital condyle in an area 12 mm wide and 20 mm long. Anteriorly, a spur of bone lies in the middle of this area of insertion. Posteriorly, the muscle extends almost to the posterior extremity of the occipital condyle.

Digastric: The posterior belly of the digastric arises from an area on the temporal bone 8 mm by 17 mm immediately lateral to the rectus capitis lateralis. No groove or marking is associated with this area on the skull base. Posteriorly, it extends as far as the posterior limit of the occipital condyle. Immediately posterior to this muscle attachment, lying between the rectus capitis lateralis and posterior belly of the digastric, the most anterior part of the superior oblique muscle inserts onto the occipital bone.

Styloid muscles: An ossified styloid process 15 mm long, and firmly attached to the cranial base, was present; the process gradually became cartilaginous towards the tip. The base of the process was only 3 mm anterior to the lateral part of the rectus capital lateralis, and about 10 mm medial to the

midline axis of the digastric origin on the cranial base. Two muscles arose from the temporal bone lateral to the process and their attachments extended laterally on the temporal bone for 8 mm. It was not possible to identify or dissect these muscles due to the poor condition of the soft tissues, but they most probably represented the origin of the stylohyoid and styloglossus muscles.

SUMMARY OF RESULTS OF THE DISSECTION STUDY

The results of this study demonstrate that there are several anatomical features consistently associated with the pongid skull base that differ markedly from the anatomical descriptions of muscles associated with the modern human skull base.

In all the specimens dissected, the longus capitis muscle arose from an elongated area on the basioccipital, being larger in the anteroposterior direction than mediolaterally. The bony eustachian process of the temporal bone was in all cases associated with the origin of the tensor palati muscle, and part of the levator palati muscle usually lay against the medial surface of the process. In addition, in several specimens a fibrous ligament was also associated with this process. In the larger specimen of Gorilla gorilla dissected, the levator palati arose from a larger area of the eustachian process than in the other specimens dissected (should this be found to be a general finding in Gorilla gorilla, it might account for the much larger eustachian process in this animal). Where it was possible to identify the cranial attachments of the superior constrictor in the specimens dissected, the muscle extended from the basioccipital posterolaterally to the petrous apex immediately medial to the levator palati muscle, and thereafter remaining in close approximation with the skull base as it passed anteriorly to the region of the medial pterygoid plate.

The posterior belly of the digastric muscle was not associated with any

groove, fossa or bony marking in any of the specimens dissected, but was consistently positioned immediately lateral to the rectus capitis lateralis muscle.

The muscles of the mastoid and nuchal regions were always relatively large and were especially complicated in the specimen of Pongo pygmaeus dissected. The same specimen showed an additional occipital insertion for the rhomboid muscles.

CHAPTER 11.

Results of the metrical study of fossil hominid crania and of the study of muscle markings on the cranial base of certain fossil hominids.

The results of the fifteen linear measurements and the two angles for the fossil sample are given in Table 9. The crania are grouped in the table according to accepted taxonomic attribution. or treated as individual specimens. Crania have been included in this latter group either because their taxonomic attribution is still uncertain, or, in the case of TM 1517 and Taung, because the remains of the former are fragmentary and the latter is immature. The results are also presented in a series of two-dimensional plots (Figures 43-47). In each of these plots the mean values for the linear and angular measurements of Homo sapiens and Gorilla have been included at the top of each figure for comparison. The results will be considered in the four groups used in Table 9.

1. Adult fossils attributed to Australopithecus africanus (Sts 5, Sts 19, Sts 25 and MLD 37/38) (Figure 43)

The skull base diagrams of all these fossils more closely resemble the pattern of the pongid samples than they do the modern human sample. Overall, they are small and the bilateral structures all lie relatively close to the midline, except for the carotid canals which are relatively further apart than those of the pongid taxa. Compared to the pongids, the length of the cranial base as a whole is reduced in Sts 19, 25 and MLD 37/38, but rather less so in Sts 5, and the foramen magnum is closer to the bitympanic line. The bitympanic width is also reduced in comparison with the pongid taxa, but not to the extent it is in the modern Homo sapiens sample; this may be related to a reduction in the size of the masticatory apparatus (Dean and Wood, 1981a). The petrous axes are aligned more sagittally than in the

CRANIAL BASE DATA FOR HOMINID FOSSILS

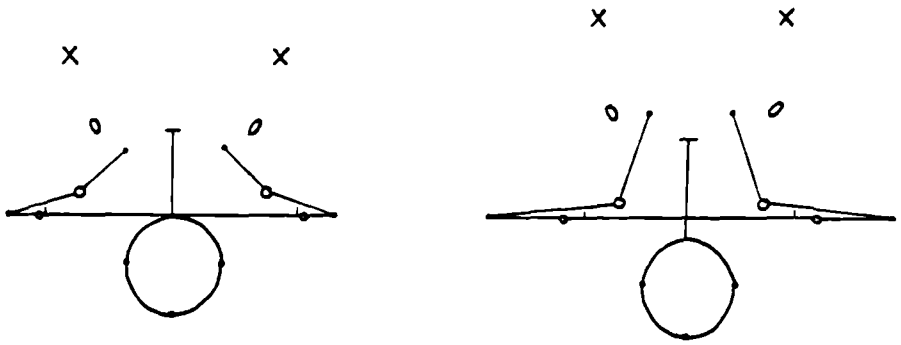
TABLE 9.

		WIDTH								LENGTH							ANGLES	
		TP-TP	SP-SP	CC-CC	FO-FO	IT-IT	SM-SM	PA – PA	FM-FM	BS-OP	TP-CC	CC-PA	SB-BS	IT/IT-TP/TP	FO/FO-TP/TP	IT/IT - BS	α	β
* FOSSIL GROUPS																		
Australopithecus africanus	Sts 5	92	66	48	48	50	69	26	24	29	23	24	25	53	28	50	65	103
	Sts 19	89	63	50	44	(49)	68	25	22	27	22	20	20	41	22	39	59	98
	Sts 25	(90)	-	42	44	50	-	(26)	-	-	19	19	-	(43)	37	(40)	72	104
	MLD 37/38	97	62	47	47	50	69	25	25	28	26	24	22	47	24	48	60	93
Australopithecus (Paranthropus) bolsei and robustus	KNM-ER406	132	79	65	58	61	85	29	32	29	34	30	29	57	30	53	44	100
	OH5	122	72	59	57	64	83	29	26	27	36	24	28	60	31	55	45	102
	SK47	100	68	51	43	(54)	78	22	20	27	25	20	12	45	23	37	45	107
Homo erectus	KNM-ER3733	120	79	58	61	66	89	35	32	35	29	26	27	55	30	57	48	104
	KNM-ER3883	115	78	57	54	69	84	31	26	31	29	25	24	55	28	52	55	105
	OH9	123	84	67	57	76	92	30	-	-	25	28	30	60	30	60	50	108
INDIVIDUAL FOSSILS																		
	KNM.ER407	102	64	53	40	60	73	28	28	29	25	23	21	47	24	40	49	112
	KNM-ER732	(100)	-	(36)	(41)	(60)	-	(14)	-	-	33	19	-	50	-	-	45	105
	KNM-ER1470	131	-	(60)	(45)	70	-	(25)	-	(30)	(30)	(25)	(25)	(56)	(27)	(56)	(45)	(105)
	KNM-ER1813	103	66	55	(51)	(65)	72	(20)	(26)	29	19	24	(22)	44	24	45	46	95
	KNM-ER1805	118	72	48	44	60	78	(20)	-	-	32	(20)	-	60	42	(58)	46	112
	OH24	(103)	67	48	49	61	72	23	25	29	30	20	(16)	45	28	38	54	108
	SK847	(98)	(60)	(44)	(46)	(62)	(63)	(21)	-	-	23	20	-	49	31	41	50	110
	TM1517	(118)	(66)	(50)	(41)	(61)	(67)	(18)	-	-	(35)	(21)	-	63	35	(57)	42	115
	TAUNG	(54)	-	(38)	(36)	(44)	-	(15)	-	-	9	(14)	(16)	29	18	32	50	90

* I. All linear measurements in mm
II. All angles to the nearest degree
III. Measurements in parentheses are either estimates, or, in the case of widths, were derived by doubling measurements taken on one side only.

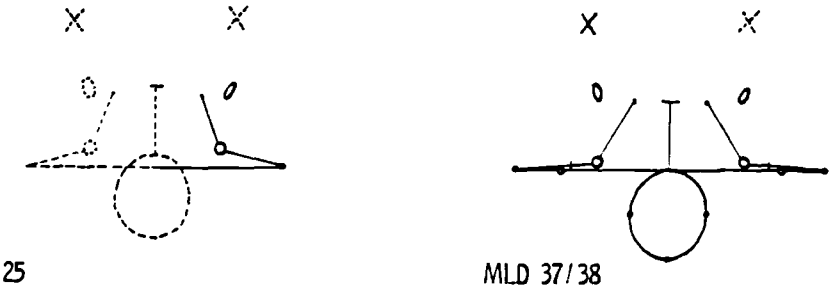
Figure 43

Skull base diagrams of fossils attributed to Australopithecus africanus with Homo and Gorilla for comparison



Homo Gorilla

Sts 5 Sts 19



Sts 25 MLD 37/38

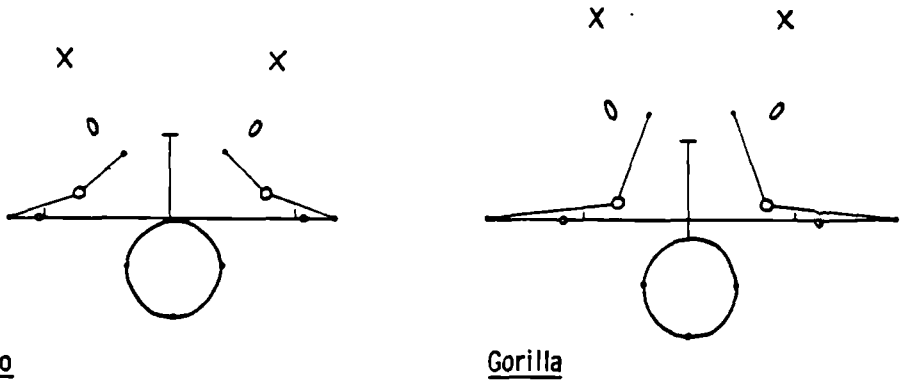
I All diagrams are to scale and are reduced to 40% of life size

II Landmarks in Homo and Gorilla correspond to their mean value

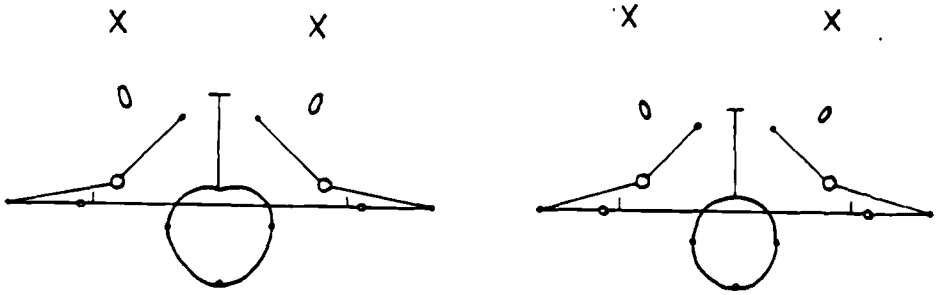
III Where the position of a landmark can only be estimated, or is derived by mirror imaging the preserved side, it is marked by a broken line

Figure 44

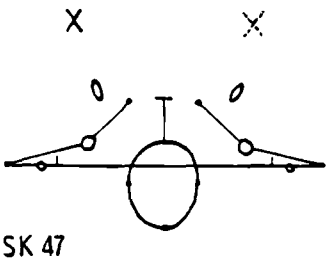
Skull base diagrams of fossils attributed to Australopithecus (Paranthropus) boisei and robustus with Homo and Gorilla for comparison



Homo Gorilla



KNM-ER 406 OH 5



SK 47

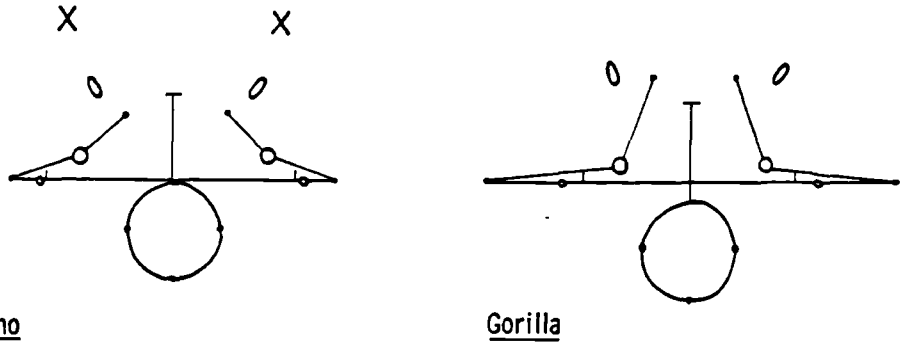
I All diagrams are to scale and are reduced to 40% of life size

II Landmarks in Homo and Gorilla correspond to their mean value

III Where the position of a landmark can only be estimated, or is derived by mirror imaging the preserved side, it is marked by a broken line

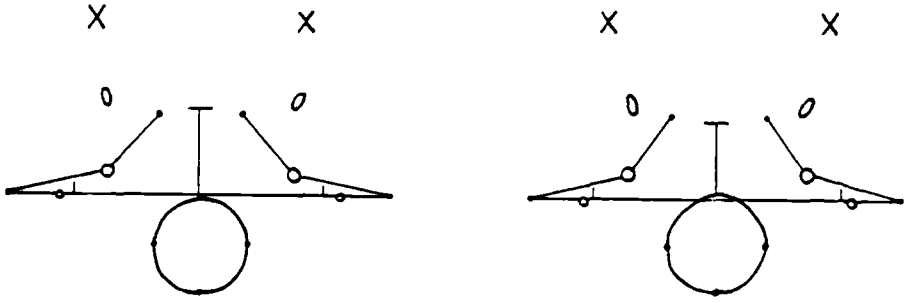
Figure 45

Skull base diagrams of fossils attributed to Homo erectus with Homo and Gorilla for comparison



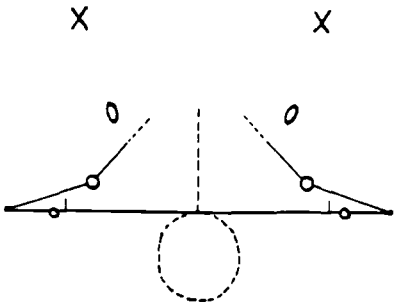
Homo

Gorilla



KNM-ER 3733

KNM-ER 3883



OH 9

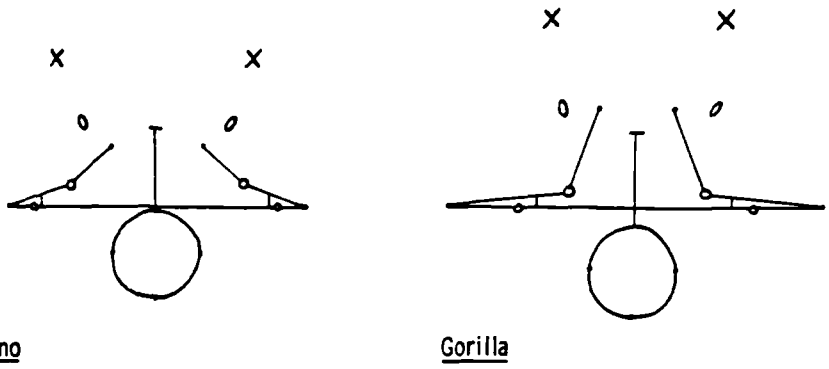
I All diagrams are to scale and are reduced to 40% of life size

II Landmarks in Homo and Gorilla correspond to their mean value

III Where the position of a landmark can only be estimated, or is derived by mirror imaging the preserved side, it is marked by a broken line

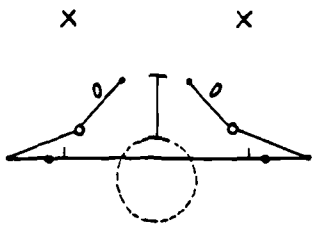
Figure 46

Skull base diagrams of Plio-Pleistocene Hominid Crania from East Africa with Homo and Gorilla for comparison

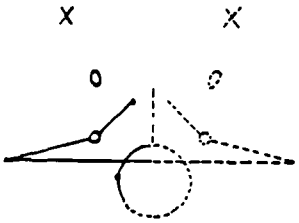


Homo

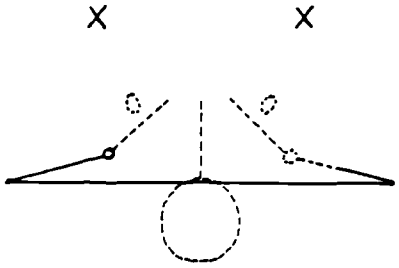
Gorilla



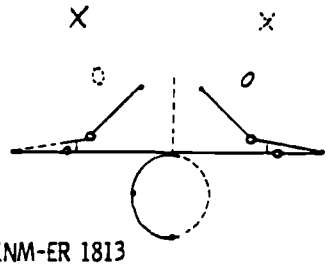
KNM-ER 407



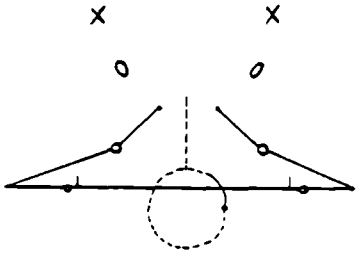
KNM-ER 732



KNM-ER 1470



KNM-ER 1813



KNM-ER 1805

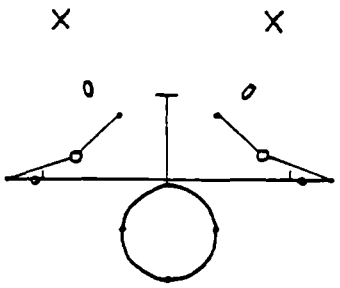
I All diagrams are to scale and are reduced to 40% of life size

II Landmarks in Homo and Gorilla correspond to their mean value

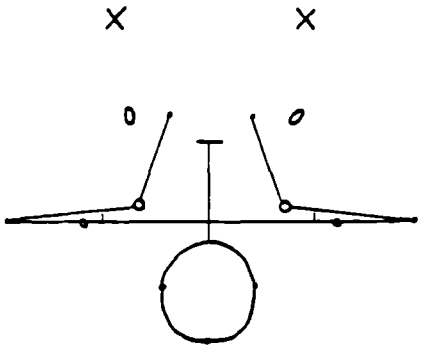
III Where the position of a landmark can only be estimated, or is derived by mirror imaging the preserved side, it is marked by a broken line

Figure 47

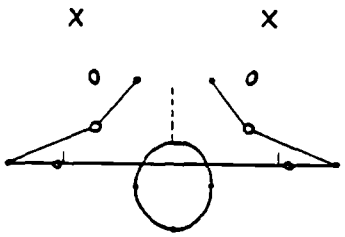
Skull base diagrams of individual Plio-Pleistocene Hominid Crania from South Africa with Homo and Gorilla for comparison



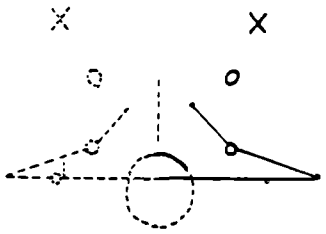
Homo



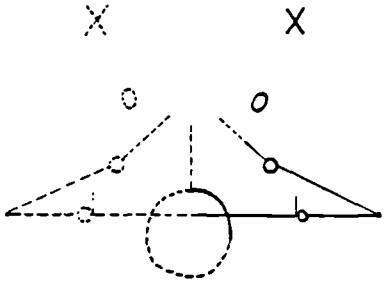
Gorilla



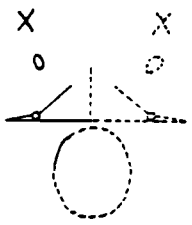
OH 24



SK 847



TM 1517



Taung

I All diagrams are to scale and are reduced to 40% of life size

II Landmarks in Homo and Gorilla correspond to their mean value

III Where the position of a landmark can only be estimated, or is derived by mirror imaging the preserved side, it is marked by a broken line

modern Homo sapiens sample, but slightly less so than in the pongid taxa. The range for α in the 'gracile' australopithecines is 59^{o} to 72^{o}. This is comparable to the distribution of values in Pongo ($\alpha = 60^{o} - 71^{o}$), but it is at the lower end of the ranges of the Pan and Gorilla samples. The orientation of the tympanic axis is very similar to that in the pongid taxa, but the range within the 'gracile' group also overlaps the range of the modern Homo sapiens sample.

The more sagittal orientation of the petrous axis is the most notable contrast between the cranial base patterns of the 'gracile' australopithecines and modern Homo sapiens, and the shortened tympanic plates and reduced skull base length of the 'gracile' australopithecines are features which contrast with the pattern typical of the pongids.

ii. Relatively complete fossils attributed to Australopithecus boisei and robustus (KNM-ER 406, OH 5, SK 47) (Figure 44)

The cranial base diagrams of this group of fossils are distinct from the pattern of both the comparative pongid sample and the 'gracile' australopithecines, and they share some features of the cranial base pattern of the modern Homo sapiens sample. Overall, the cranial base of this group is large and particularly wide across the lateral extremities of the tympanic plates. The cranial base is shorter than that of the pongids and the anterior margin of the foramen magnum is positioned well in front of the bi-tympanic line, unlike either the modern humans or the 'gracile' australopithecines and the pongids. The orientation of the petrous axis closely resembles that of the modern human sample and values for this angle in the 'robust' group of fossils fall within the middle of the range, $\alpha = 31^{o} - 55^{o}$, for modern Homo sapiens. The orientation of the tympanic axis also resembles that of the modern human group, but values for β for the 'robust' group fall towards the lower end of the modern human range. This is almost certainly due to the long tympanic plates reducing the value of β in the 'robust'

group. The bicarotid canal width (CC - CC) in KNM-ER 406 and OH 5 exceeds the modern human mean value, but whereas in the Homo sapiens sample the bi-infratemporal fossa width (IT - IT) is disproportionately wider than the other bilateral landmarks, this is not the case in the 'robust' group. There appears to have been little reduction in the length of the body of the sphenoid bone in the 'robust' crania compared with the pongid taxa (if sphenoid length is taken as equivalent to the distance IT/IT - FO/FO in Figures 43 - 47).

iii. Fossils attributed to Homo erectus (KNM-ER 3733, 3883 and OH 9) (Figure 45)

The cranial base pattern of this group of fossils resembles that of modern Homo sapiens. They differ from the 'robust' group and resemble the Homo sapiens sample in two ways. The first is the position of the foramen magnum which lies approximately on the bi-tympanic line, and not well in front if it, as it does in the 'robust' australopithecine fossils. The second is the broadening of the sphenoid so that the bi-infratemporal fossa width (IT - IT) exceeds the biforamen ovale and bicarotid canal widths (FO - FO and CC - CC); this trend is, however, not as marked in Homo erectus as it is in Homo sapiens. The petrous axis in Homo erectus is more sagittally orientated than in Homo sapiens and the 'robust' australopithecines, with the values of α falling at the upper end of the Homo sapiens range; in contrast, the values for β fall towards the bottom of the range for Homo sapiens. This is partly due to the relatively long tympanic plates in Homo erectus, which have the effect of reducing the value of β and accentuating the difference between the tympanic and petrous axes.

iv. Individual Plio-Pleistocene hominid crania (KNM-ER 407, 732, 1470, 1805 and 1813, OH 24, SK 847, TM 1517 and Taung) (Figures 46 and 47)

For convenience, these fossils have been divided into four groups on the basis of similarities in cranial base patterns; no other implications are intended at this stage and the groupings are not intended to be taxonomic units.

KNM-ER 407, KNM-ER 732, OH 24 and SK 847

This group of fossils shows a combination of features, some of which are characteristic of the 'robust' australopithecines, and others which are seen in Homo erectus and in the modern Homo sapiens sample. The position of the foramen magnum relative to the bitympanic line resembles that in the 'robust' sample, but the relatively wide and foreshortened sphenoid bone are features of Homo. The value of α for the orientation of the petrous axis is 49° in KNM-ER 407, 45° in KNM-ER 732, 54° in OH 24 and 50° in SK 847. With the exception of KNM-ER 732, these values are slightly higher than those for the 'robust' sample and within the range for Homo erectus. There is little to distinguish between the cranial base patterns of these four fossils except that the petrous angle and the sphenoid length/width ratio of OH 24 and Sk 847 are more indicative of the pattern seen in Homo erectus.

KNM-ER 1470 and KNM-ER 1813

The cranial base patterns of these two fossils resemble those of the Homo erectus group. The foramen magnum lies on the bitympanic line, the angle β is low and the angle α high. The sphenoid bone is foreshortened but wide across the infratemporal fossa at the base of the greater wings. Two obvious differences between these two crania are the relatively short sphenoid, and the smaller overall size, of KNM-ER 1813.

KNM-ER 1805 and TM 1517

These fossils combine a relatively long cranial base and a foramen magnum which is positioned well in front of the bitympanic line. The values for angle β are high, with the tympanic axis being orientated further forwards than it is in modern Homo sapiens, but the angles α are comparable to the mean values for both the 'robust' australopithecines and the modern Homo sapiens sample. The presumed position of the spheno-occipital synchondrosis in KNM-ER 1805 is some way behind the line connecting the posterior margins of the foramen ovale, thus suggesting that the sphenoid body may have been longer than indicated by the IT/IT - FO/FO distance in Figure 46. Apart from the relatively high value for angle β, and a marked narrowing of the biforamen ovale width (a feature which they share with KNM-ER 732), the basicrania of these two specimens are similar in shape to those attributed to the 'robust' australopithecines.

Taung

Developmentally, this juvenile specimen is not directly comparable with the other fossil hominids used in this study and for this reason it is considered separately in the discussion section.

Results of the study of soft tissue markings on the cranial base of the fossil hominids

The results presented in this section are based upon notes and measurements taken directly from the original fossil hominid specimens used in this part of the study and from observations made on the painted duplicate plaster casts. Photographs of the painted casts of specimens Sts 5, MLD 37/38, SK 47, KNM-ER 406, 1805, 1813, OH 5 and OH 24 are included as Plates 10 and 11.

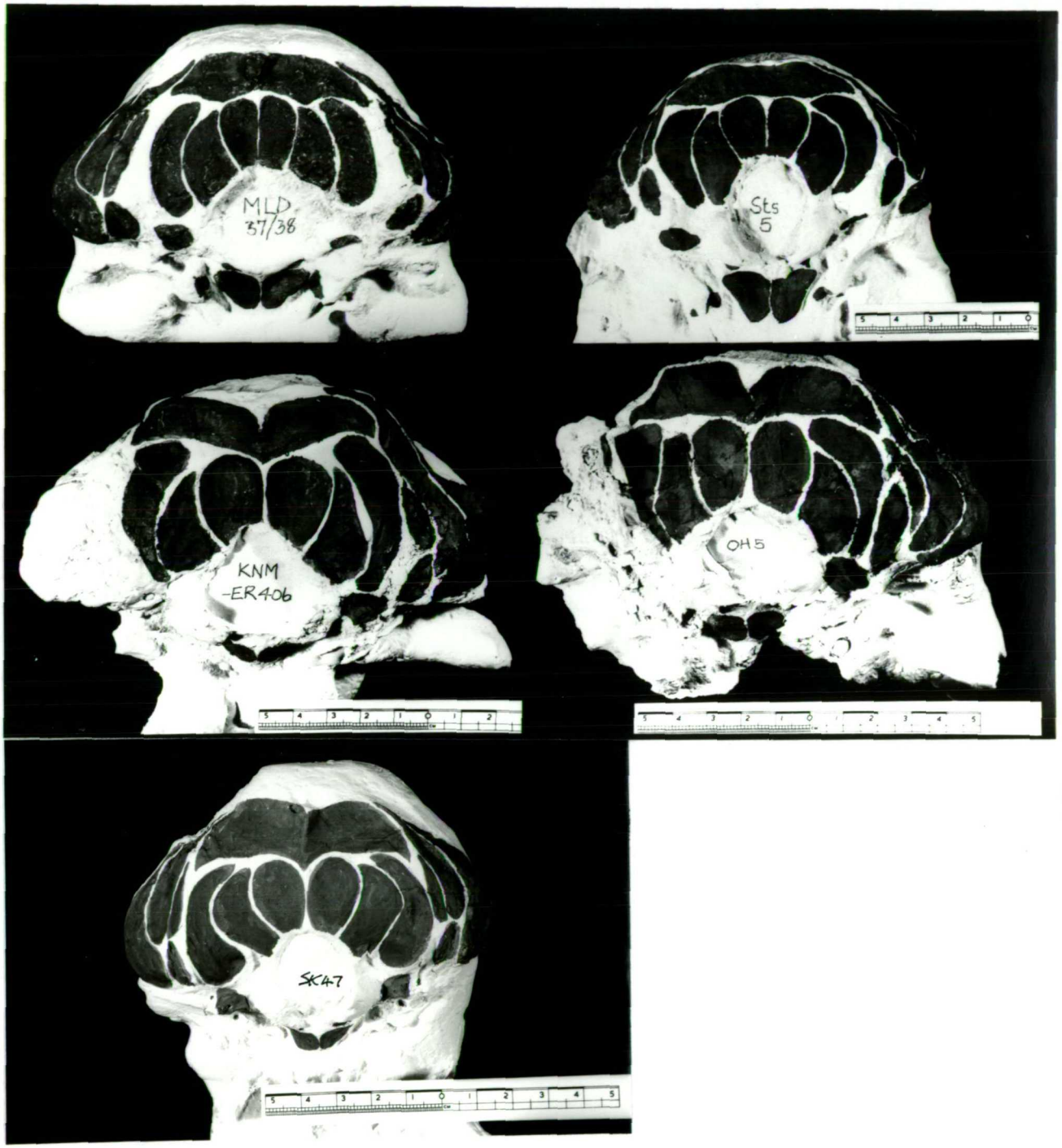


Plate 10. Outlines of muscle markings on the cranial base of MLD 37/38, Sts 5, KNM-ER 406, OH 5 and SK 47.

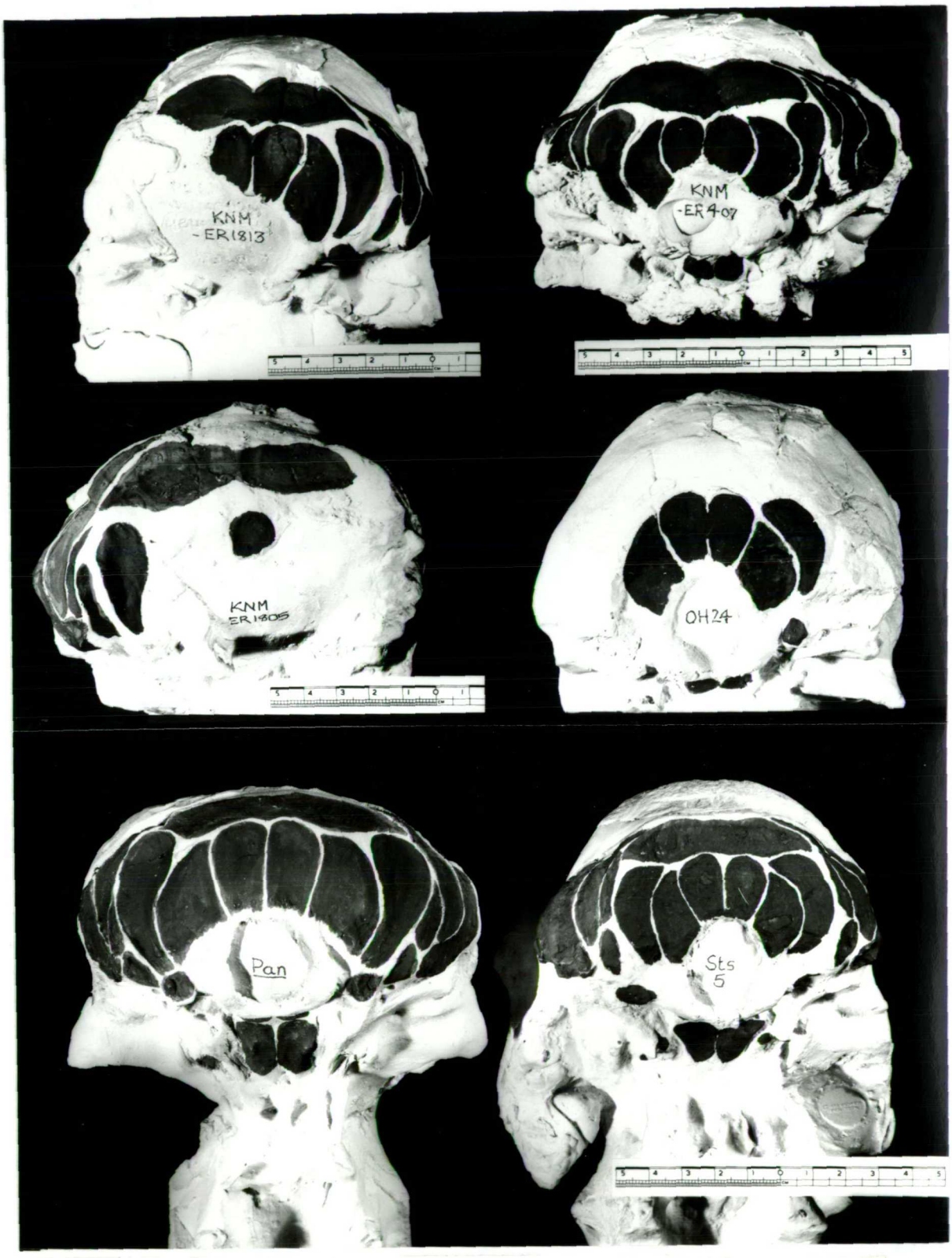


Plate 11. Outlines of muscle markings on the cranial base of KNM-ER 1813, 407, 1805 and OH 24 with a specimen of Pan together with Sts 5 for comparison.

Prevertebral and upper pharyngeal muscle markings

Two of the eight fossils, MLD 37/38 and Sts 5, stand apart as being distinctly pongid-like in this region. Both of these specimens have elongated bony ridges on the basioccipital for the insertion of the longus capitis muscles. These ridges are about 18 mm long in both specimens, and are narrower anteriorly. It seems likely that the area of insertion for each longus capitis muscle in these two specimens measures about 18 mm x 12 mm (this area is intermediate in size between the areas of insertion of the adult male specimens of Pan and Pongo dissected in this study). The basioccipital in MLD 37/38 and Sts 5 is considerably wider immediately anterior to the foramen magnum than it is at the spheno-occipital synchondrosis. There is also some indication that the rectus capitis anterior muscles mark the basioccipital immediately anterior to the occipital condyles; these impressions lie some 10 mm from the midline. The shape of the basioccipital and the presumed markings for the rectus capitis anterior are features of the two fossils not seen in the pongid crania.

Another important feature of this region in MLD 37/38 and Sts 5 is the marked bony eustachian process present on the temporal bones of both specimens. This process measures about 5 mm in diameter at its base and lies immediately inferior to the opening of the cartilaginous eustachian tube. In the light of the findings of the dissection study, it seems likely that this process gives origin to the tensor palati, and perhaps also to a part of the levator palati, the main origin for the levator palati being more medial on the underside of the apex of the petrous temporal bone. These markings all lie lateral to the markings for the longus capitis muscle. The carotid canals in both specimens also lie lateral to the posterior part of this ridge on the basioccipital. Sts 5 has a well marked scaphoid fossa, measuring about 3 mm by 11 mm, with its centre placed 17 mm anterior to the base of the eustachian process.

KNM-ER 1805 and 1813 are damaged in the region of the basioccipital but none of the other remaining five specimens studied show the same combination of features seen in Sts 5 and MLD 37/38. There is a slight raised ridge on the basioccipital of the larger specimen, OH 5, but none on another large specimen, KNM-ER 406. In these two specimens the limits of the markings for the longus capitis are difficult to determine, but they are probably about 12 or 13 mm long and about 10 mm wide. The smaller specimens, OH 24, KNM-ER 407 and SK 47, (more comparable in size to MLD 37/38 and Sts 5) have shorter basioccipitals and it is unlikely that the area of insertion of the longus capitis muscle could have exceeded 10 mm by 10 mm in any of these specimens. There is some indication that the maximum width of the longus capitis attachment on the basioccipital of OH 24 lies horizontally across the skull, as it tends to in modern Homo sapiens. What markings there are for the rectus capitis anterior muscle in OH 5, OH 24, KNM-ER 406, 407 and SK 47 indicate that these muscles are well separated and lie immediately anterior to the occipital condyles in these specimens. Specimen OH 24 has a small eustachian process on the left temporal bone and a scaphoid fossa measuring 3 mm by 9 mm on the left side. In all the fossils in which the carotid canals can be identified, they lie lateral to the posterior limit of the attachment of the longus capitis muscle.

Mastoid and deep mastoid muscle markings

The muscle markings in this region of the cranial base are difficult to interpret, particularly so in the fossil hominid crania.

Where there is some indication of the insertion of the rectus capitis lateralis in the hominids, it appears to be placed lateral to the occipital condyle and does not extend further anteriorly than the midpoint of the anteroposterior axis of the condyle, However, in the pongid specimens dissected, the attachment of this muscle appears to extend further anteriorly relative to the occipital condyles. Two specimens, KNM-ER 407 and

KNM-ER 1805, are damaged in this region and there is no indication about the position of the rectus capitis lateralis. In the two larger specimens, KNM-ER 406 and OH 5, the bony areas for the rectus capitis lateralis are about 12 - 13 mm in diameter but in the smaller specimens, OH 24, KNM-ER 1813, Sts 5, MLD 37/38 and SK 47, the area associated with this muscle is nearer 7 - 8 mm in diameter.

All the fossil hominid specimens studied (except OH 24 and KNM-ER 407 which are damaged in this region) show evidence of a digastric groove or fossa. In all the specimens this groove or fossa is positioned postero-lateral to the position of the rectus capitis lateralis and the styloid pit. This contrasts with the finding in the pongid dissections that the posterior belly of the digastric leaves no bony marking and is positioned immediately lateral or anterior to the rectus capitis lateralis. In OH 5, KNM-ER 1805 and KNM-ER 406, the approximate size of the fossa is 20 mm by 8 mm but in the smaller specimens, MLD 37/38, Sts 5, KNM-ER 1813 and SK 47, the digastric fossa is smaller and measured about 15 mm by 6 mm. KNM-ER 1805 and OH 5 stand out from all the other specimens as having a very marked juxtamastoid eminence running between the medial part of the digastric fossa and the lateral margin of the area for attachment of the superior oblique muscle. Two specimens, KNM-ER 1813 and SK 47, have a well marked groove medial to the digastric fossa which may be for the occipital artery. This groove is either less clear, or missing, in the other specimens.

The larger specimens, KNM-ER 406, 1805 and OH 5, have extensive bony areas on the cranial base for the attachment of the longissimus capitis, splenius capitis and sternocleidomastoid muscles. These three specimens have marked nuchal crests to support muscle attachments in this region. In the smaller specimens, these three muscles were apparently less massive and gained attachment from a reduced bony area. They still tend to form a marked superior nuchal line, but it does not form a crest in any of these remaining specimens.

Nuchal and deep nuchal muscle markings

The muscle markings in this region of the skull base are greatly reduced in size when compared with the same region in the pongids. This difference is very noticeable when the smaller specimens, Sts 5, MLD 37/38, SK 47 and KNM-ER 407, are compared with Pan. The distance between the most lateral markings of the superior oblique muscles in Pan or Pongo is about 100 mm across the nuchal planum, whereas in OH 5 or KNM-ER 406 this distance is only 75 mm, and only 65 mm in the smaller fossils. The size and relationships of the rectus capitis posterior major, rectus capitis posterior minor and superior oblique muscles are very similar in the smaller specimens. The three specimens, OH 5, KNM-ER 406 and KNM-ER 1805, all appear to have marked bony ridges or even crests in the region of the superior oblique muscle, but this may be related to the overall size of the crania. Three specimens, OH 24, KNM-ER 407 and Sts 5, have no external occipital protuberance in the region on the attachment of the semispinalis capitis muscle, which suggests a 'pongid-like' absence of the ligamentum nuchae, but MLD 37/38, SK 47 and KNM-ER 1813 among the smaller specimens do have a well marked external occipital protuberance, and KNM-ER 406 and KNM-ER 1805 among the group of larger specimens also have a small external occipital protuberance in this region. OH 5 stands apart from all the other eight specimens in having a very well developed external occipital protuberance which projects about 10 mm from the nuchal planum.

Summary of the results of the study of soft tissue markings on the cranial base of fossil hominids

The two specimens attributed to Australopithecus africanus (MLD 37/38 and Sts 5) show some bony surface markings characteristic of the pongids in the prevertebral and upper pharyngeal regions. These features do not appear to be shared by any of the other fossils described in this study. All

the fossils studied have posteriorly positioned carotid canals relative to the longus capitis muscle markings, and all of the specimens show evidence of a digastric groove or fossa situated posterolateral to the rectus capitis lateralis and the styloid apparatus.

The smaller specimens have reduced mastoid and nuchal muscle markings, whereas the larger specimens have more complicated cresting associated especially with the superior oblique and the muscles attached to the nuchal crest. None of the fossil hominids shows any of the very large areas of attachment for the deeper nuchal muscles that are present in the pongid taxa.

PART IV DISCUSSION

CHAPTER 12.

Discussion.

One of the major aims of this thesis was to document any consistent patterns in the size and shape of the cranial base and to relate these patterns to the findings about comparative soft tissue anatomy in extant hominoids. In addition, data about postnatal ontogenetic changes occurring in the cranial base of extant hominoids were to be used, along with the results of the preceding two studies, to explore the observed patterns of comparative basicranial anatomy in the fossil hominids and examine the extent to which ontogenetic changes reflect any observed phylogenetic trends in the fossil hominids studied.

The results of this thesis are discussed in four sections. The first section deals with previous studies of the cranial base and discusses the findings of human and comparative studies and their relevance to this study. The second section relates the findings of the adult metrical study of the cranial base and that of the fossil hominids to those of the soft tissue dissection study and the analysis of the muscle attachment of the fossil hominids, and discusses the probable underlying functional adaptations that link the two sets of results. The third section is a discussion of the growth study of the cranial base and a general assessment of the value of information about growth processes, including the insight they provide into evolutionary change and phylogenetic trends among fossil hominids. The fourth section examines the results of the study of the individual fossil hominid crania in the light of the preceding three sections.

Previous studies of the hominoid cranial base

Many studies of the hominoid cranial base have been made in the sagittal plane. One problem that has arisen in previous comparative studies of the cranial base is the difficulty of defining a set of stable homologous landmarks

that can be used in several different groups of primates. Lestrel and Moore (1978) have previously discussed the difficulty of describing a complicated anatomical region such as the cranial base in a wide range of primate groups without a reliable set of homologous landmarks. Ashton (1957), Scott (1958, 1963) and Cramer (1977) are among those who have drawn attention to the drawbacks of using the nasion as an indicator of the plane of the foramen caecum (the anterior end of the cranial base) in the non-human primates because of the upward remodelling which occurs during growth. Others have drawn attention to the intra-taxonomic variation that occurs during growth in the regions of the sella turcica and the spheno-occipital synchondroses and the implications that this has for comparative studies of the cranial base. Latham (1972) and Gould (1977), for example, have discussed the upward remodelling that occurs in the region of the sella turcica in man and it is possible that growth changes occurring in the cranial base angle in other primates may in part be due to an absence of the upward remodelling that occurs in this region in modern man. There is also evidence that growth changes occurring at the spheno-occipital synchondrosis may be different in modern man and the non-human primates. Sirianni and Van Ness (1978) have shown that in Macaca there is more growth posteriorly at the inferior border of the synchondrosis than there is superiorly, so that the plane of the spheno-occipital synchondrosis seen in norma lateralis appears to rotate and so contribute to the 'opening out' and increase in the cranial base angle during growth. There is no suggestion in the literature that this occurs in man. These studies indicate that the problem of choosing homologous midline landmarks in the sagittal plane is a difficult one and suggest that there may be advantages to studying the cranial base in norma basilaris.

The relationship between changes occurring in the sagittal and basal planes of the cranial base are not widely discussed in the literature.

However, there is good evidence to suggest that an increase in cranial base flexion accompanies the changes associated with basal compression apparent when the cranial base is viewed in norma basilaris. The studies of Bateman (1954), DuBrul and Laskin (1961), Schulter (1976) and DuBrul (1977) have all provided data that link a more flexed skull base, as seen in the sagittal plane, with compression in the basal plane. These effects include a shortening of the cranial base and an inward rotation of the petrous pyramids. Björk (1955), Moss (1958) and Laitman (1977) have also shown that when there is a decrease in cranial base flexion in the sagittal plane, there is an accompanying downward rotation of the clivus, foramen magnum and cerebellum. These studies suggest that there is a relationship between cranial base flexion in the sagittal plane and compression of the cranial base.

The problem of what processes govern cranial base flexion and basal compression is less clear. Huxley (1863) suggested that there was a relationship between facial prognathism and cranial base flexion and since then Huxley himself (1867), Sonntag (1924), Weidenreich (1947), Björk (1950), Scott (1958) and Cramer (1977) have all presented evidence to support such an association in primates. Other workers have suggested that the effects of expansion of the neurocranium, both during human phylogeny and ontogeny, play a part in determining the degree of cranial base flexion (Moss 1958 and Beigert 1963). Another view is that the type of habitual posture, and the relative proportions of the neurocranium to the viscerocranium also have some influence upon the degree of cranial base flexion (DuBrul 1950, Schultz 1955, Beigert 1957, 1963, DuBrul and Laskin 1961, Le Gros Clark 1977 and DuBrul 1977).

The results of this thesis have demonstrated the existence of a consistent set of morphological patterns in the cranial base of extant hominoids and fossil hominids. The literature surveyed in this thesis suggests that

the patterns seen in norma basilaris can be plausibly related to known patterns of cranial base flexion in the sagittal plane but that detailed comparative studies in the sagittal plane alone may be limiting. The many functional demands that underlie these patterns are complicated but must nonetheless reflect the adaptive modifications that have occurred in the skulls of hominoids. The advantages of studying the skull base in norma basilaris are several. Anatomical landmarks other than those in the midline can be used and these include structures with important and obvious functional associations such as the styloid process and the nervous and vascular foramina of the cranial base. These landmarks are also easily identifiable on the cranial base of many primates. Measurements on the base of the cranium are easier to make than many that involve endocranial landmarks in the sagittal plane and few fossils are complete enough to make any measurements other than those that utilize landmarks on the exocranial surface of basicranium.

By concentrating on the cranial base in norma basilaris the problem of choosing homologous and stable landmarks has been overcome and, by concentrating upon structures that can be identified easily, it has been possible to include as many as twenty early fossil hominid specimens in this study of the hominoid cranial base.

The adult metrical, fossil hominid and dissection studies

The patterns of cranial base morphology presented in the results of the adult metrical study of this thesis are most conveniently discussed by considering the factors that relate to variations in the width and length of the basicranium.

The anteriorly positioned foramen magnum and occipital condyles of the modern human cranium are associated with a lateral displacement of the adjacent vascular foramina and styloid apparatus. This forward position of the foramen magnum is clearly one factor that contributes to an increase

in the width between the carotid canals, stylomastoid foramina and styloid processes. The modern human skull, however, stands apart from the other comparative groups, and many of the fossil specimens used in this study, in that it has a greatly enlarged neurocranium. This in turn has had an important effect upon the size of the vascular foramina, especially the size of the carotid canals and the jugular foramina which, with the possible exception of the Homo erectus sample, are considerably larger in the modern Homo sapiens sample than in any of the other crania studied. The large size of the foramina may also account for the fact that in the modern human cranium they are positioned more anteriorly relative to the foramen magnum than they are in, for example, the 'robust' australopithecines. In the comparative pongid samples, as well as in the 'robust' and 'gracile' australopithecines and fossil specimens attributed to early Homo, the size of the vascular foramina is small and any widening of the bilateral structures in this region of the skull base is most likely due solely to the forward migration of the foramen magnum and occipital condyles compressing them laterally. A very marked anterior migration of the foramen magnum, such as that found in the 'robust' australopithecines, results in a wide bicarotid canal width but in these specimens the carotid canal is small in diameter and is not displaced anteriorly relative to the foramen magnum, as it is in the Homo sapiens and Homo erectus crania.

Weidenreich (1951) has suggested that the length of the tympanic plates may be related to the degree of development of the masticatory apparatus and such an association appears to hold true in the comparative pongid samples and the 'robust' australopithecines. The modern human cranium has markedly shortened tympanic plates and because of the additional lateral migration of the more medial soft tissue structures of the cranial base, there is even less space available for the intervening soft tissues than there would otherwise be.

The dissection study has clearly demonstrated that in the pongid taxa the posterior belly of the digastric muscle generally has a wide origin on the cranial base. Nevertheless, it is lateral to the rectus capitis lateralis and styloid apparatus as it is in modern man. There is, however, some evidence from the dissection study to suggest that the rectus capitis lateralis muscle has migrated forward with the foramen magnum and occipital condyles in modern man, changing its relationship with the digastric which remains more posteriorly positioned on the cranial base. The combined evidence of the metrical and dissection study suggest that, when the space available for the posterior origin of the digastric muscle is greatly reduced, as it is in modern man because of the widened medial soft tissue structures and reduced bitympanic and bimastoid widths, a groove or fossa is formed to accommodate this muscle at its origin and a mastoid process develops to increase the available surface area for the more superficial muscles of the mastoid region. The width between the styloid apparatus is sufficiently great, and the superficial mastoid muscles are sufficiently medial, to bring about the development of a groove or fossa in all the fossil hominids studied. The results of this study suggest therefore that, even in the large 'robust' australopithecines there has been sufficient lateral migration of the vascular foramina and styloid apparatus to cause the more laterally positioned digastric muscle to take origin from an elliptical groove. Olson (1981) attaches considerable importance to the morphology of the mastoid region and digastric fossa in Homo sapiens and the extant pongids for his analysis of certain fossil hominids, and suggests that changes resulting from habitual upright posture are responsible for the morphology of this region and for the formation of the digastric fossa in man. However, Olson argues that a relocation of the nuchal planum downwards results in a decrease in the total surface area available for the attachment of the rectus capitis posterior major, rectus capitis posterior minor and superior oblique muscles. (This

is unlikely as the foramen magnum has moved anteriorly, the occipital region has expanded considerably and the muscles of the suboccipital triangle have become reduced in size (Adams and Moore 1975) following the more efficient poise of the head in habitually bipedal hominoids.) Nevertheless, Olson (1981) suggests that the lateral expansion of the muscles in the suboccipital region of Homo sapiens results in "the lateral displacement of both the origin of the digastric muscle and the occipitomastoid crest", the subsequent restriction of space resulting in the formation of a deep fossa on the temporal bone. The posterior belly of the digastric runs anteriorly and that of the superior oblique posteriorly and it is unlikely that one could displace the other laterally. The styloid apparatus, however, runs adjacent to and immediately medial to the posterior belly of the digastric and any lateral displacement of the styloid apparatus must influence the position of the origin of the digastric muscle more than the muscles of the suboccipital triangle.

The forward migration of the foramen magnum and occipital condyles also appears to have brought about changes in the region of the prevertebral and upper pharyngeal muscles. A reduction in the length of the basioccipital has resulted in a spreading of the rectus capitis anterior muscles so that in modern man and, most probably in all the fossil hominids studied, these muscles lie futher from of the midline, and not as they do in the pongid specimens dissected, close together and immediately anterior to the foramen magnum. The insertion of the longus capitis muscle has also become reduced in length and, in crania where the basioccipital is markedly reduced in length, it lies with its long axis horizontally across the basicranium. It is noteworthy that the 'gracile' australopithecines (Sts 5 and MLD 37/38) appear to retain the long anteroposterior insertion of the longus capitis muscles seen in the pongid taxa.

In modern man the pharynx is expanded superolaterally and compressed anteroposteriorly and at its upper end it extends posteriorly to the region of

the carotid sheath. This may be due to the combination of increased size of the jugular foramina and carotid canals, and their subsequent anterior displacement relative to the foramen magnum, as well as to the reduced length of the basioccipital and reduced size of the longus capitis muscles. The position of the foramen magnum, however, has no direct reflection upon the angles as measured in this study because these angles only relate the position of the carotid canals to the petrous apices and the bitympanic line and not to the position of the foramen magnum. These angles remain largely independent of the position of the foramen magnum, but instead are dependent upon the position of the carotid canals.

The sphenoid bone is intimately related to both the neurocranium and the viscerocranium. The cranial base patterns of the comparative samples and the fossil hominid specimens indicate that the body of the sphenoid is long and narrow in the pongids and australopithecines, but that it becomes shorter and wider in Homo, so that modern Homo sapiens have the shortest but widest sphenoid bones. Widening of the sphenoid is almost certainly associated with an increase in cranial capacity and especially to an increase in the size of the temporal lobes of the brain in the middle cranial fossa. Shortening of the body of the sphenoid is more complicated, but may be associated with retrusion of the face and be involved in the cranial base compression that occurs in association with flexion of the cranial base. It may be that the whole bone has been remodelled laterally following a widening of the anterior cranial fossa and a retrusion of the face occurring together. The form of the basioccipital of the 'gracile' australopithecines, which is wide posteriorly and narrow anteriorly, suggests that a widening of the nasopharynx occurred before widening more anteriorly. The influence of the forward position of the foramen magnum seems then to have preceded the influence of neural expansion, facial retrusion and cranial base flexion, which are the probable factors underlying changes in the anterior part of the nasopharynx and sphenoid bone.

The attachments of the levator and tensor palati muscles to the temporal bone in two 'gracile' australopithecines (Sts 5 and MLD 37/38) closely resemble those observed in the pongid specimens dissected. The narrow anterior nasopharynx is associated with a temporal origin for both these palatal muscles. The large eustachian process in these specimens, similar to that found in the gorilla, suggests that, like the gorilla, both the levator and tensor palati muscles took origin from the process and that the more medial levator palati muscle had an additional origin from the inferior surface of the petrous temporal bone. It is interesting to note that the orang utan has a wider cranial base than the gorilla or the chimpanzee and that in the orang utan the eustachian process is much smaller and is sometimes absent, and that only the tensor palati takes origin from it, the levator palati arising from the petrous apex, though its lateral surface is still closely associated with the eustachian process. In modern man, the tensor palati arises from the sphenoid bone, the origin of this muscle having migrated laterally. However, the apex of the petrous temporal bone has rotated medially away from the position of the two muscles, possibly under the influence of the cranial base compression. As a result, the levator palati muscle in modern man occupies a more lateral position on the petrous apex. This change in relationship between the muscles and the temporal bone has not, however, been sufficient to move the origin of the levator palati onto the sphenoid bone. Nonetheless, there is evidence in the literature demonstrating that in modern man it arises laterally from the region of the carotid sheath and petrous temporal bone (Rowan and Turner 1956).

None of the other groups of fossils has such a narrow anterior nasopharynx, or such a marked eustachian process as the 'gracile' australopithecines, but several fossil specimens, including TM 1517, OH 24 and the Homo erectus crania described by Weidenreich (1934, 1951), do possess a small eustachian process, and Zuckerman et al (1962) have drawn attention to "a small petrous spine" present in some modern human crania. It seems

reasonable to associate the large eustachian process in the 'gracile' australopithecines with the narrow nasopharynx and unflexed elongated cranial base; features that also exist in the gorilla and chimpanzee.

The greatly reduced nuchal musclature of Homo sapiens and the fossil hominids is more than likely related to habitual upright posture and a more efficient balancing of the head upon the spinal column. In some of the fossil hominids there has also been a reduction in the size of the viscerocranium, which has further reduced the forces required to support the head in a horizontal position. Compared with the massive nuchal muscles of the pongids, those of the 'gracile' australopithecines appear very much reduced and it is interesting to note that the prevertebral muscles in the 'gracile' australopithecines, presumably also involved in the balance of the skull, are still relatively large and pongid-like, markedly more so than the prevertebral muscles are in the larger 'robust' australopithecines. Large ridges on the basioccipital indicate well developed longus capitis muscles which are powerful flexors of the head. Large occipital ridges have also been reported in some species of sabre toothed cats where Turnbull (1977) has suggested that they are associated with the specialized dental adaptation. It may well be that these ridges in the 'gracile' australopithecines simply reflect the surrounding pongid-like morphology in the region of the basioccipital and bear no relationship to any functional adaptation affecting the cranial base.

Another, more likely, explanation hinges on the argument that the longus capitis muscles in the 'robust' and 'gracile' australopithecines may be the only powerful flexors of the head, whereas this is not the case in modern Homo sapiens. In Homo sapiens there is a well developed mastoid process and Krantz (1963) has demonstrated that the sternocleidomastoid muscles act as powerful flexors of the head. When the head is tilted back in modern man the tips of the mastoid processes swing in front of the axis of rotation

of the occipital condyles. Contraction of the sternocleidomastoid muscles so bring the head back into the horizontal position. Thus in Homo sapiens the sternocleidomastoid muscles act with the longus capitis muscles as flexors of the cranium. In the 'gracile' and 'robust' australopithecines, however, the mastoid process is less well developed and lies behind the axis of rotation of the occipital condyles so that when the head is tilted back the longus capitis muscle has also to oppose the action of two additional powerful nuchal muscles, the sternocleidomastoid muscles.

The relative size of the longus capitis muscles may then simply reflect the weight of the skull in front of the axis of rotation of the occipital condyles, which is the only force acting with these muscles to bring the head forward. In the 'robust' australopithecines the face is massive and may be the reason that the size of the insertion of the longus capitis muscles are much reduced. In the 'gracile' australopithecines, though there is more facial prognathism, the face is less massive and there may be a greater need for large longus capitis muscles to oppose the nuchal musclature when the head is pulled forwards from a 'tilted back' position, or for support when rising from a horizontal position.

The specimens used in this study, from both the comparative groups and the fossil hominids, exhibit a large range of variation in body size. Although the mean values of each linear measurement reflect this, the cranial base patterns described in the results section are, however, apparently independent of these differences in body size. Within one group of specimens that share a similar cranial base pattern, the comparatively large specimens of Gorilla share a similar cranial base pattern with smaller specimens of Pan and Pongo and specimens, even smaller, of Australopithecus africanus. Within the other group of specimens that share a broadly similar cranial base pattern there is also a considerable range in body size. This group includes Homo habilis, Homo erectus, Homo sapiens and the robust australopithecines.

It seems reasonable to conclude that the cranial base patterns apparent in norma basilaris are largely independent of the effects of differences in body size.

The growth study of the hominoid cranial base

The importance of differential growth as a mechanism for morphological change during evolution has long been recognised and attention has been focused upon this problem in two ways.

One approach has been to formulate general laws of growth derived from observed regularities during the growth of individuals (Thompson 1917, Huxley 1932). These laws have been used to demonstrate systematic transformations and constant differential growth ratios. Huxley's allometric formula for example ($Y = bx^{\alpha}$) has been widely applied to describe proportional size changes during evolution (for example, see Robb 1935), but this general approach to the problem of growth cannot provide information about the mechanisms of evolutionary changes that have taken place.

Another example of this general approach has figured more prominently in the literature dealing with human evolution. It has been suggested that human evolution is characterised by a general retardation of the growth processes during ontogeny, so that juvenile features are apparent later in the ontogeny of man than they were in our ancestors. Bolk (1926), for example, insisted that all the "essential" features of modern man were the result of developmental retardation. More recently Gould (1977) has revived these ideas and once again suggested that modern man is "essentially neotenous". Gould believes that human beings are neotenous because a "general temporal retardation of development has clearly characterized human evolution" (p. 365). Retardation, as Gould sees it, does not necessarily entail the physical retention of juvenile features. For example, retardation (or retention) of the foetal growth rate confined to the gonads results in 'hypermorphosis'. Another example is the human brain which

Gould (p. 365) regards as paedomorphic "because it has increased by prolonging to greater times and larger body size (even past birth) the characteristic positive allometry generally confined to foetal stages in primates and other mammals". Schultz (1949, p198) also writes that "human ontogeny is not unique in regard to the duration of life in utero but that it has become highly specialized in the striking postponement of completion of growth and the onset of senility".

Gould effectively argues that either a decrease or an increase in the relative rate of growth can represent a retention of foetal growth characteristics (Gould 1977, p.365). He does, however, accept that there can be exceptions to the [retention of foetal growth patterns, for example the proportions of the lower limbs of modern man that are indisputably the result of an acceleration in the growth rate during development (p.383). Løvtrup (1978) has suggested that prolongation rather than retardation would be a more suitable generalization to apply to human development. Clearly Gould's broader definition of neoteny ("the retention of formerly juvenile characters by adult descendants produced by a retardation of somatic development") is a broader approach to the concept of neoteny in human evolution. Nevertheless, this general approach to the relationship between phylogeny and ontogeny, although proposing a general mechanism, retardation, does not provide any information about the specific sites of differential growth that might underlie evolutionary changes.

The second approach to differential growth and evolutionary change has been to explore the effects of changes occurring at primary growth centres and compare the resulting morphological variations with similar morphological changes that can be identified as evolutionary adaptations in the fossil record. Differences in form and proportion among fossil and living groups have been related to changes in the relative rates of growth during individual development (Baer 1954). Similarly, differences in the size and shape of the skulls of hominoids must result from differences in the rates of growth of

the components of the neurocranium and the viscerocranium. DuBrul (1950, 1977), Baer 1954 and DuBrul and Laskin (1961) have adopted this approach and provided some indications about the possible mechanisms that might underlie morphological changes in the skulls of rodents and primates. (A comprehensive review of the literature and critical analysis of growth centres in the cranial base is given by Hoyte, 1975.)

The comparative cross-sectional growth study in this thesis was carried out with a view to providing information about two problems. The first was how closely growth patterns in the cranial base of the three pongid taxa compared with what is already known about growth patterns in the cranial base of modern man. The second was to see if, by extending this second approach to the problem of differential growth and evolutionary change outlined above, it was possible to do more than generalize about the mechanisms underlying morphological change in the hominoid cranial base. Several other questions arise in connection with this second problem: Can one do more than generalize as Bolk and Gould have done that the human skull is "essentially neotenous" ? How far does ontogeny of the human cranial base represent a parallel of phylogenetic changes that have occurred during human evolution ? What are the roles of developmental retardation and acceleration in bringing about the changes in shape that have occurred in the cranial base of hominoids ? These basic problems used to formulate the growth study in this thesis form a useful framework with which to discuss the results. However, some consideration of the methods used to measure growth changes in this and other studies is necessary before any objective interpretation of the results can be made and these methods will be discussed first.

Many cross-sectional growth studies of the cranial base have used the state of eruption of the dentition to divide specimens into developmental subsets, for example Zuckerman (1955), Ford (1965), Ashton (1957), Fenart et Deblock (1973), Cramer (1977), Laitman (1977), Laitman et al (1978). The

major drawbacks of this method of ageing individual crania have been outlined in Chapter 7 but there are other important considerations to be borne in mind when interpreting cross-sectional data. Cross-sectional data are widely recognised as being unsuitable for any detailed analysis of developmental growth curves (Tanner 1962). Using chronological age in cross-sectional studies is likely to be more misleading than using a developmental measure of age because of the large variation in development that occurs with chronological age and because of the fact that developmental events within, for example, the skeletal system tend to be better correlated with each other than with chronological age (Talmers 1952). It follows then that by adopting the developing dentition as a measure of relative developmental age in this study, information about the probable growth curves of each hominoid sample have been maximised as far as possible. However, one fact that should be borne in mind is that the developing dentition suffers less from the effects of malnutrition than does skeletal development (Tanner 1962). This 'buffering' of dental development means that any individuals thrown off their growth curves by the effects of malnutrition would probably have lower values for cranial variables than would be expected for their relative dental developmental ages. Any specimens suffering from malnutrition at the time of death and inadvertantly included in this study might have abnormally low values for their relative dental age and it is important that this should be considered when unusual results are obtained. The small numbers of individual human and pongid specimens available for the first two years of postnatal life in this study must also be taken into consideration when large increases in the rate of growth are observed during this period. Willoughby (1978) has drawn attention to longitudinal data relating to weight increase with age in primates and notes that the early growth period of the primates has been greatly extended but that "the gorilla does not exhibit the initial postnatal spurt of growth shown by man and the chimpanzee, but increases in weight at an almost uniform rate during the first few years". Gavan

(1954) also presents longitudinal growth data for the chimpanzee which, in contrast to the results of this study, tends to indicate that the postnatal growth spurts for man and the chimpanzee are very similar in magnitude. None of this data, however, is for the cranial base and there are no studies that provide information for longitudinal growth data for the cranial base in Gorilla, Pan or Pongo. Nevertheless, these more general findings should be borne in mind when the results of this study are interpreted.

Data about growth in primates have also been presented in other ways. Schultz (1940, 1941) measured change in form by means of an index or ratio in which one measure was expressed as a proportion of another. Gavan (1953) demonstrated that growth curves for trunk height in man and the chimpanzee are remarkably similar when age is expressed as a percentage of the total growth period and trunk height is expressed as a percentage of the adult value. Thus, by plotting variables against trunk height instead of chronological age, some of the difficulties that arise when comparing growth curves in man and the chimpanzee may be overcome. These arise primarily because of the big difference in the final size of the adults and because of the different durations of the growth period. Gavan (1966) later demonstrated that the relative growth rate for sitting height in primates (and even dairy cattle!) is the same. Primates, however, have simply increased the duration of growth and man has one unique feature, the pubertal growth spurt.

These methods of measuring growth changes are important, but a major aim of this growth study was to compare the characteristics of the growth curves of man and the pongids and describe the mechanisms that result in different adult cranial base patterns. One advantage of adopting relative dental developmental age as a method of measuring growth changes is that it is easier to compare the findings of this study with previous cross-sectional growth studies of the hominoid cranial base. Many features of growth curves that create problems in other comparative growth studies, such as

differences in final adult size and differences in the total growth period, form an important part of the results in this study and need to be expressed in a comparable and comprehensive manner.

Growth of the cranial base in Homo sapiens and the three pongid taxa

An important finding of the results of the comparative growth study of this thesis is that they confirm there is a basic similarity in the pattern of growth in the cranial base of modern man and the three pongid taxa. Ford (1958) has demonstrated that in man the cribriform plate completes its growth at about 2 years and thereafter decreases in size very slightly, and it appears that this also occurs in the pongids. The studies of Zuckerman (1955) and Ashton and Spence (1958) have shown that in man and the pongids the foramen magnum ceases to grow after eruption of the first permanent molars and this has been confirmed in this study. In addition, the distance between the nasion and the foramen caecum and the length of basioccipital continue to increase throughout the growth period in both man and the pongids (Zuckerman 1955, Ashton 1957 and Scott 1958).

Some differences appear to exist in the region of the spheno-ethmoidal articulation and the spheno-occipital synchondrosis in hominoids. Ashley Montague (1943) noted that the frontal bone failed to intervene between the ethmoid and the sphenoid bones of the orang utan. In this study, the length of the cribriform plate in the orang utan always corresponded exactly to the total length of the ethmoid bone, suggesting that the posterior ethmoidal air cells are absent in the orang utan (this has previously been noted by Cave and Haines, 1940). In Gorilla and Pan posterior ethmoidal air cells do appear to be present and growth in this region is associated with their proliferation, as well as with a high incidence of the frontal bone intervening between the ethmoid and sphenoid in the anterior cranial fossa (Ashley Montague, 1943). Growth at the spheno-ethmoidal articulation in the primates is complicated and difficult to record (see Hoyte 1975) and a more detailed

analysis of this region in hominoids generally, would be useful. Growth at the spheno-ethmoidal articulation in man appears to cease at about 6 years (Ford 1958) and total growth in the length of the body of the sphenoid bone between the ages of 4 and 16 years only amounts to about 5 mm (Nakamura et al, 1972). Latham (1972) has noted that no increase in length occurs between the posterior wall of the sella turcica and the sphenoidal surface of the spheno-occipital synchondroses after 2 years of age in man, although there is some remodelling in the region of the sella turcica. There appears then to be some intra-specific variation in this region in hominoids, but growth in length of the sphenoid and ethmoid bones appears to be mostly completed by 5 or 6 years in both man and the pongids.

Studies of the human cranial base in the sagittal plane have shown that the cranial base angle in man first decreases after birth (George 1978), and then either increases slightly or decreases slightly until growth of the skull is completed (Björk 1955, Zuckerman 1955). Comparative data for the three pongid taxa (Ashton 1957, Fenart and DeBlock 1973 and Cramer 1977) has shown that the cranial base angle in Gorilla, Pan and Pongo increases steadily throughout the whole of the growth period. This study confirms these earlier findings, but also demonstrates the large range of variation in this angle present during the whole growth period in all three pongid taxa. Despite the difficulties that exist in making comparisons of the cranial base in the sagittal plane between Homo sapiens and the pongid taxa, due mostly to the complicated differences in remodelling and the growth characteristics of this region, it does seem that there is a general relationship between the cranial base angle γ and the petrous angle α. The petrous angle α increases when the cranial base angle γ becomes less flexed and increases. This is further evidence that basicranial compression results in horizontally orientated petrous pyramids. The only exception to this is an increase in the petrous angle in Homo sapiens after about $3\frac{1}{2}$ years, which is not

accompanied by a definite increase in the cranial base angle $\propto$. However, it may be that a real increase is masked by the remodelling which occurs in the region of sella as reported by Latham (1972).

The relationship between ontogeny and phylogeny of the cranial base in hominoids

This problem is best discussed by considering the general features of the growth curves that contribute to differences in the human and pongid cranial base patterns and then by following this with a more detailed consideration of the features of the growth curves that are related to fundamental differences between the pongid cranial base and the human cranial base.

The most important general differences between the human and pongid growth curves noted in this study are the lengthening or prolongation of the human growth curve and the tremendous spurt of growth during the first year of postnatal human development that results in the majority of growth of the human cranial base being completed early in the growth period. Whereas the typical pongid growth rate remains relatively constant during the whole of the growth period, growth of the human cranial base is largely complete by 6 years of age.

Detailed differences between the human and pongid growth curves are most easily considered by describing separately differences in width and length and in orientation of the petrous and tympanic parts of the temporal bone. Greater widths across the bilateral structures of the human cranial base appear to result from the greater initial rate of growth during the immediate postnatal years and are not simply due to the general prolongation of the growth period. The only measurement in width that is wider in the pongids than in man is bitympanic width, and this must in part be due to values greater than those of Homo already being present at birth in the pongid taxa, rather than to a fundamental difference in this growth pattern. The shorter

lengths of the human cranial base (both total length, IT-IT/TP-TP and length of the basioccipital, SB-BS) result from a reduction in the early postnatal spurt and an early cessation of growth in Homo, the long pongid cranial base resulting from both an increase in rate of growth and the additional growth that continues after growth has ceased in Homo. This increase in length of the basioccipital in pongids also reflects the backward migration of the foramen magnum that is occurring throughout the growth period.

Growth changes in the two angular measurements made in norma basilaris (α and β) follow a broadly similar pattern in both man and the pongids, both increasing in value by about 10^{o} during the total growth period. What is important, however, is that the values of α and β at birth in man and the pongids, like the values for bitympanic width, already differ from one another so that the adult human values for α and β cannot be regarded as belonging to a stage of development in the pongids that has become 'fixed' due to retardation. It could be argued that retardation of the growth changes occurring in the angles α and β has occurred earlier, sometime during foetal development, but growth in all taxa is still occurring at a comparable rate after birth and both Stark and Kummer (1962) and Stark (1973) have previously drawn attention to the fact that the human and chimpanzee foetuses do show important basic differences even before birth. It is also interesting to note that the data provided by Fenart and Deblock (1973) indicate that there are already differences in the cranial base angle in Pan paniscus and Pan troglodytes at birth and it is possible that, once again, differences apparent at birth underlie differences in the mean adult values. In summary, it is clear from the present study that basic differences in the length of the tympanic plates and the orientation of the petrous temporal bones and tympanic plates between man and the pongids exist soon after birth.

The results of this study suggest that when the growth rates and growth periods for the bones of the cranial base in man and the pongids are

compared, differences in the patterns of the adult cranial bases can be attributed to a combination of decreases and increases in growth rate as well as to differences in size and shape that are present at, or soon after, birth. The greater human values for IT-IT, Fo-Fo, CC-CC, SP-SP and SM-SM all appear to result from the marked increase in growth rate that characterises the human growth curve for the cranial base region during the first few postnatal years. The smaller human values for IT-IT/TP-TP and SB-BS result from the combined effect of a reduced postnatal spurt and an early cessation of growth in Homo. Differences in the degree of orientation of the petrous and tympanic parts of the temporal bone, as well as some of the differences in width between the extremities of the tympanic plates in man and the pongid taxa, result at least partly from morphological differences present soon after birth.

The results of this thesis suggest that no one fundamental change in growth pattern underlies the basic difference observed in adult hominoid cranial base shape. Both general differences in the growth curves and local changes in growth rate are responsible for the pattern of the adult cranial base in Homo sapiens. It would then be an over-simplification, even with the broader concepts of Gould in mind, to regard the whole of the human cranial base as a 'neotenous' or 'retarded' form of the pongid cranial base.

The cranial base patterns of the fossil hominids show a combination of pongid and human characteristics, none of them entirely pongid or entirely human, but it seems clear that no one simple change in growth pattern is likely to underlie all the changes that have occurred during human evolution.

The form of the cranial base in fossil hominids

The sample of adult crania attributed to Australopithecus africanus shows a combination of features, some typical of the extant pongid taxa and some typical of modern Homo sapiens. The posterior part of the cranial

base shows features that probably result from the forward position of the foramen magnum and occipital condyles. These include a lateral displacement of the vascular foramina and styloid apparatus and the formation of a digastric groove medial to the mastoid process. The value of the petrous angle$\propto$ is slightly lower in the 'gracile' australopithecines than it is in the extant pongids and this is most probably due to the lateral displacement of the carotid canals. Anteriorly the cranial base is slightly foreshortened but remains essentially 'pongid-like'. In general, Sts 19 and 25 follow the pattern of MLD 37/38 in having a more foreshortened sphenoid than Sts 5. Sts 19 has both a shortened sphenoid and the least sagittally orientated petrous axis of the group, and both of these features make it the most '*Homo*-like' of the sample.

The suggestion that Sts 19 may not be a typical 'gracile' australopithecine is not a new one. When Sts 19 was first described in detail, and referred to as skull No. 8 (Broom and Robinson, 1950, p.31), the authors referred to the "human" proportions of the posterior cranial fossa. In the same monograph Schepers (1950, p.102) commented that "the manner in which the cerebellum has come to be shifted forward and below the cerebral occiput is most striking. The general arrangement is that found for the human brain, especially in *Homo sapiens*." Clarke (1977) considered the morphology of the cranial base of Sts 19 in detail and suggested there were several features of the morphology of the temporal and sphenoid bones that were *Homo*-like. He considered the possibility that Sts 19 should be excluded from *Australopithecus africanus* but also noted the alternative, that the "more *Homo*-like characteristics of Sts 19 compared to the more pongid-like characteristics of Sts 5 might be indicative only of a wide range of variation among the Sterkfontein *Australopithecus* population". The results of the metrical analysis in this thesis suggest that Clarke's second interpretation is the more probable one.

Three crania were chosen to represent the 'robust' australopithecines in this study. The two larger crania, KNM-ER 406 and OH 5, were chosen because of their completeness and the subadult 'robust' australopithecine cranium SK 47 was included because it is the only 'robust' australopithecine specimen from South Africa with a more or less complete and undistorted cranial base. Despite its immaturity, Ashton and Zuckerman (1952b, p.615) noted that in SK 47 "the muscular markings of the occipital region of the fossil are far more pronounced than in either man or the chimpanzee, and are as well developed as in gorillas of corresponding age". In addition, they remark that the inion and external occipital crest in SK 47 are better marked than those of adolescent gorillas and chimpanzees. These observations run counter to those of Olson (1978) and lend support to the results of this thesis which suggest that, if it had reached full adulthood, SK 47 would have come to resemble the two adult 'robust' australopithecine crania very closely. Olson (1978) has drawn attention to cranial and dental features of SK 47 which he considers are hominine, but the cranial base metrical data presented in this thesis are not sufficiently discriminatory on their own to make any significant contribution to deciding the relative strengths of the hominine and 'robust' australopithecine affinities of SK 47. Nonetheless, some features such as the anteriorly situated foramen magnum, suggest a closer association with the 'robust' taxon and, for the purposes of this analysis, SK 47 has been regarded as a specimen of Australopithecus robustus.

Howell (1978) has maintained a separation at the species level between specimens recovered from Kromdraai and Swartkrans. The incomplete cranial base of TM 1517 from Kromdraai resembles the cranial base pattern of the robust' sample used in this study more closely than any of them resemble the pattern in the 'gracile' australopithecines. The affinities of TM 1517 are with the 'robust' group, but it differs from them in having a eustachian process, a more elongated cranial base and a larger angle β .

Its cranial base pattern also closely resembles those of KNM-ER 732, a possible small-bodied female of the 'robust' taxon, and KNM-ER 1805.

The foramen magnum and occipital condyles in the 'robust' australopithecines are positioned much further forward than in the 'gracile' australopithecines or early Homo. This may possibly underlie the wide separation of the carotid canals and the low value of the petrous angle $\propto$. The vascular foramina however are small and presumably reflect the relatively small cranial capacity of this group. As a result of the small cranial capacity, the structures of carotid sheath lie lateral to the posterior part of the longus capitis muscle and the carotid canals are not displaced anteriorly, as they are in Homo sapiens and Homo erectus. In addition, the cranial base is markedly flexed in the 'robust' australopithecines and the resulting basal compression has probably further contributed to the low petrous angle. The extremely long tympanic plates in the 'robust' australopithecines may have contributed to a reduction in the tympanic angle which might otherwise be higher and closer to the values for Homo erectus. The retruded facial skeleton, flexed cranial base and anterior position of the foramen magnum may all contribute to the similarities between the cranial base pattern of the 'robust' australopithecines and that of Homo sapiens. One interpretation of this apparent example of parallel evolution is that different functional demands have been responsible for similar modifications in the basicranium of these two forms (DuBrul 1977). It is possible that the large neurocranium and small facial skeleton of Homo sapiens, and the small neurocranium and massive facial skeleton of the 'robust' australopithecines may have resulted in a similar pattern of basicranial anatomy in these two forms.

The calvarium KNM-ER 407 and the cranium KNM-ER 732 were recovered from the lower part of the Upper Member at Koobi Fora in North Kenya (R.E. Leakey, M.G. Leakey and Behrensmeyer 1978). Both specimens show marked postorbital constriction and have expanded and heavily pneumatized mastoid regions. The mandibular fossae are wide and extend laterally well

beyond the sides of the cranial vault. Although the specimens are incomplete, they have sufficient anatomical areas in common to suggest that they should be considered as belonging to the same taxon. A preliminary assessment of KNM-ER 407 leads to the conclusion that it "probably is either a gracile species of Australopithecus or else a very early representative of Homo" (R.E. Leakey 1970). Since then, Wolpoff (1978a) has espoused the former proposition, but the latter has received no support. From the outset, KNM-ER 732 was considered as a possible small-bodied female of Australopithecus (R.E. Leakey 1971) and, although these reports made no specific attribution, the clear inference was that the material should be referred to Australopithecus boisei (R.E. Leakey 1970, 1976). Since these preliminary pronouncements two substantial reviews of the fossil hominid evidence from Koobi Fora concurred with the judgement that KNM-ER 407 and 732 are probable female sexual dimorphs of Australopithecus boisei (Howell 1978 and Wood 1978).

It is clear from the cranial base diagrams (Figs. 14-18) and the results in Table 9, that neither KNM-ER 407 nor 732 have a basicranium which resembles that of the 'gracile' australopithecines. The forward position of the foramen magnum in both crania is a feature which resembles the 'robust' australopithecine group and, in view of the features of the frontal and malar region which KNM-ER 732 shares with specimens attributed to Australopithecus boisei (Wood 1978 and in press), the evidence from the cranial base suggests that the most parsimonious taxonomic placement of these two specimens is within Australopithecus boisei.

The three crania attributed to Homo erectus in this thesis (KNM-ER 3733, KNM-ER 3883 and OH 9) show a cranial base pattern similar to that of Homo sapiens. The foramen magnum is close to the bitympanic line but not well in front of it as it is in the 'robust' australopithecines. The sphenoid bone is foreshortened and wide. Weidenreich (1947) has demonstrated that the cranial base, viewed in the sagittal plane, is less flexed

in Homo erectus than it is in modern Homo sapiens (and probably also less flexed than it is in Australopithecus robustus). This may account for the higher petrous angle α in Homo erectus and is an indication that the medial rotation of the petrous temporal bone under the influence of basicranial compression may not be as great as it is in Homo sapiens and Australopithecus robustus. The carotid canal, however, is displaced further from the foramen magnum than it is in the 'robust australopithecines, and this may be related to the increased size of the vascular foramina. The long tympanic plates in Homo erectus also accentuate the angle formed between the tympanic and petrous axes by reducing the angle β, but nonetheless the styloid apparatus is just as laterally displaced as it is in Homo sapiens.

The cranium KNM-ER 1470 was recovered from the Lower Member of the Koobi Fora Formation. Its age, based on isotope dating, is between about 1.8 Myr. and 2.8-3.0 Myr. (Drake, Curtis, Cerling, Cerling and Hampel 1980, Gleadow 1980, McDougall, Maier, Sutherland-Hawks and Gleadow 1980) and magnetostratigraphic evidence suggests that it may be close to 2.4 Myr. old (Hillhouse, Ndombie, Cox and Brock 1977). Initial assessments suggested that the affinities of KNM-ER 1470 were with Homo (R.E. Leakey 1973 and Wood 1976) but Walker argued for caution and quite properly stressed the features, particularly of the face, which are shared between KNM-ER 1470 and Australopithecus (Walker 1976). Subsequent reviews have favoured its inclusion in Homo habilis (Howell 1978), or treated it as a conspecific of the 'gracile' australopithecine material from Sterkfontein (Olson 1978). Evidence derived from the cranial base of KNM-ER 1470 in this study suggests that the hominid group it most closely resembles is Homo erectus. There are clear contrasts between the cranial base of KNM-ER 1470 and that of the 'gracile' australopithecines and the breadth across the infratemporal crests serves to distinguish it from 'robust' australopithecine crania. Although the overall morphology of the cranial vault and the face of KNM-ER 1470 set it apart from crania and calottes attributed to

Homo erectus, the form of its cranial base suggests that if it is assigned to Homo habilis, then the cranial base of this taxon had already developed some of the derived features we presently associate with Homo erectus and Homo sapiens.

The skull KNM-ER 1805 was recovered from just below the Okote Tuff in the Upper Member at Koobi Fora. Radiometric and magnetostratigraphic evidence all point to a date around 1.6 Myr. (Fitch and Miller 1976, Brock and Isaac 1976). Its relatively small cranial capacity, 582 ml^3, (Holloway 1978) and the combination of a compound nuchal crest and parasagittal crests have perhaps been features which have led some workers to attribute it to Australopithecus boisei (Tobias 1980). Presumably different features prompted Howell (1978) and Wolpoff (1978,b) to include KNM-ER 1805 in Homo erectus. and yet other workers to place it in a separate species of Australopithecus, either named (Olson 1978) or unnamed (Holloway 1976, R.E. Leakey 1976). The evidence from the cranial base is compatible with the inclusion of KNM-ER 1805 in either Australopithecus boisei or a species within the genus Homo, but is strong evidence against its attribution to Australopithecus africanus.

The precise strategic relationships of KNM-ER 1813 have yet to be worked out, but it is likely that it was buried in sediments in the lower part of the Upper Member, or in the upper part of the Lower Member, at Koobi Fora. Its small brain size, 509 ml^3 (Holloway 1978) and the overall shape of the cranial vault and face have prompted many workers to suggest affinities with, or its inclusion in, Australopithecus africanus (R.E. Leakey, M.G. Leakey and Behrensmeyer 1978, Holloway 1978, Olson 1978), while more hominine aspects of relative tooth size, dental morphology and tooth wear have led others to include it in Homo habilis (Howell 1978, Tobias 1980). Many features of the morphology of the cranial vault, face and dentition convincingly preclude the inclusion of KNM-ER 1813 in Australopithecus boisei (Wood 1978). Thus, with the taxonomic claims limited to its inclusion

in either Australopithecus africanus or Homo habilis, the evidence from the cranial base is crucial. If KNM-ER 1470 and OH 24 (vide supra and infra) do prove to belong to Homo habilis, the pattern of basicranial morphology in KNM-ER 1813 is strongly in favour of its inclusion in Homo and for it not to be regarded as a 'gracile' australopithecine. The foreshortening of the skull base, the widening of the sphenoid and the angulation of tympanic and petrous parts of the temporal bone are all clear and unambiguous evidence against KNM-ER 1813 being placed with the Australopithecus africanus crania described in this study.

The cranium OH 24 was found at site DK in Bed I of Olduvai Gorge. When it was found it was badly crushed, but has been skilfully restored by Dr. R.J. Clarke. The initial description pointed to the similarities between OH 24 and the Homo habilis skull, OH 13, from Bed II (M.D. Leakey, Clarke and L.S.B. Leakey, 1971). Although some differences were noted between OH 24 and OH 7 and 16, the report concluded that "beyond doubt, the new specimen represents the genus Homo as defined by Leakey, Tobias and Napier and differs fundamentally from the australopithecines". Although its inclusion in Homo habilis has been supported by some (Holloway 1976, 1978, Tobias 1980, 1981), other workers have been impressed by the similarities between OH 24 and Australopithecus africanus (R.E. Leakey 1974, Howell 1978, Olson 1978, R.E. Leakey and Walker 1980). The cranial base of OH 24 is not, however, like that of the 'gracile' australopithecines. The petrous axes are more coronally aligned and the greater width across the infratemporal crests suggests that the sphenoid in OH 24 was broader than in the Australopithecus africanus specimens.

Since the discovery that the parts of the cranium SK 847 from Swartkrans fitted with a left temporal (SK 846b) and a maxillary fragment (SK 80), the affinities of this 'composite' cranium have been in dispute. The initial assessment of its affinities considered that it differed significantly from the 'robust' australopithecines and it was regarded as Homo sp. indet.

(Clarke, Howell and Brain 1970), and a similar taxonomic conclusion was reached after a much more detailed analysis (Clarke 1977). Howell (1978) has assigned it to Homo habilis but Wolpoff has argued consistently against any taxonomic distinction between SK 847 and the 'robust' australopithecines (Wolpoff 1970, 1971, 1974). In his survey of nasal and mastoid morphology Olson (1978) regarded the 'composite' cranium as a conspecific of the 'gracile' australopithecines from Sterkfontein. In this present study, the shape of the basicranium of SK 847 has been shown to be unlike that of the 'gracile' australopithecines and thus must be counted as evidence against them being regarded as conspecific. Although the overall pattern of basicranial morphology of SK 847 shows similarities to both Homo and the 'robust' australopithecines, the relatively wide bi-infratemporal fossa breadth suggests interesting affinities with other specimens which have been attributed to Homo.

The cranial base of the Taung skull is incomplete but, because there is some disagreement about the dating and affinities of this skull, any information about the cranial base than can be derived from the results of this study is potentially important. It is probable that gingival eruption of the first permanent molars had occurred in this skull, but it is unlikely that the first permanent molars would have been in functional occlusion. This corresponds to a developmental age of about 6 years in modern man and to about 3 years 4 months in the three great apes (Dean and Wood 1981b). The results of the preceding study on the growth of the hominoid cranial base suggest that at the time of eruption of the first permanent molars, the angles α and β would not yet have reached their adult values. Of all the measurements made in this study, only the length and width of the foramen magnum of the Taung skull can be expected to approach the adult values (see also Zuckerman 1955, Ashton and Spence 1958). The value of 50° for the petrous angle α estimated for this skull is already greater than the mean value for

the adult Homo sapiens value and it also exceeds the values for the adult and subadult 'robust' australopithecine fossils included in this study. During growth of the cranial base from the time of eruption of the first permanent molars to adulthood, an increase of about 10^{o} occurs in the mean value of α in both the pongid taxa and Homo sapiens. If this is added to the existing value for α, 50^{o}, then the inference is that the petrous axis of the Taung adult would have been approximately 60^{o}. This would place it out of the observed range of the 'robust' crania and well within the range for the 'gracile' australopithecines. Tobias (1973, 1978 and 1981) has proposed that the Taung skull has closer affinities with the 'robust' australopithecines than with the 'gracile' australopithecines. It is, in addition, interesting to note that, whereas the eruption pattern of the teeth in the 'robust' australopithecines and Homo sapiens is similar (Broom and Robinson 1952, Clements and Zuckerman 1953), the eruption pattern of the incisors and first permanent molars in the Taung skull resembles the eruption pattern of the three great apes (Dean and Wood 1981b). This is also the case for Sts 24/24a and LH 2, two other juvenile mandibles attributed to the 'gracile' australopithecines (including Australopithecus afarensis). Skinner (1978, p.441) has also suggested that the mandibular arch in the Taung skull is wider anteriorly than it is in the 'robust' australopithecines and that the corpus height is equal only to the smallest 'robust' australopithecines.

These observations and results suggest that because of the general similarities that exist between the cranial base patterns of Homo and the 'robust' australopithecines, it would be unwise to try to distinguish between the two taxa solely on the evidence of the cranial base. It is, however, clear that Homo and the 'robust' australopithecines share other similarities such as the eruption pattern of the teeth (Broom and Robinson 1952, Clements and Zuckerman 1953) and the growth pattern of the jaws (Skinner 1978). This raises the possibility that the relationship between the 'robust'

australopithecines and early Homo may have been a closer one than is generally appreciated. The results of this study have also shown that there are profound differences in basicranial morphology between Homo habilis and Homo erectus on the one hand, and Australopithecus africanus on the other. The reorientation and rearrangement of the cranial base which has taken place in these early Homo taxa suggests that the relationship between Homo habilis and Australopithecus africanus may not be as close as some workers have claimed (Robinson 1972, R.E. Leakey 1974, Olson 1978, R.E. Leakey and Walker 1980). The taxonomic and phylogenetic relationships of the small brained 'gracile' crania from East Africa (e.g. KNM-ER 1813 and OH 24) remain an enigma, but the results presented here suggest that their inclusion in Australopithecus africanus may be mistaken.

The data presented in the analysis of the extant primate material and of the fossil hominid specimens in this thesis are also suitable for analysis by sophisticated multivariate analytical techniques. Whilst this is in progress and is clearly an essential step in any further analysis of this data, this type of analysis has not been included in this thesis. The purpose of this thesis has been to present a broad data base across both the soft tissue comparative anatomy and the comparative metrical data and to provide a detailed preliminary analysis of the comparative anatomy of the cranial base region. This detailed and careful inspection of the original data has by itself revealed several variables which have been shown to be useful discriminators among the fossils. Such a thorough presentation of the original data is often excluded from studies involving multivariate analysis and this makes it difficult to use data from such studies in any other way. Data presented in this study, for example, could easily by included in a later cladistic analysis of fossil hominids. The small size of many of the fossil samples and the necessity to compare these with modern extant primate samples suggest that it may be both unsound and unwise to use simpler bivariate statistical tests of affinity for much of the data presented

in this study. For these reasons only a limited statistical analysis of the data presented in this thesis has been included in the present study but more complex analyses are planned for the future.

CHAPTER 13.

Conclusions

The review of the literature of the comparative anatomy of the cranial base has demonstrated that previous emphasis upon midline structures in the sagittal plane may be limiting. The results of the adult metrical study have shown that patterns exist in the cranial base as seen in norma basilaris that can be used to distinguish between modern Homo sapiens and the three extant pongid taxa. The relatively longer and narrower cranial base of Gorilla, Pan and Pongo is clearly contrasted with the wider shorter cranial base of Homo sapiens. Two other important features are the low petrous angle of Homo sapiens and the short tympanic plates.

By employing a more objective method of ageing juvenile crania, the growth study of the cranial base has highlighted several important points about development in this region. There appear to be basic differences between Homo sapiens and the pongids in the length of time of the growth period and in the rates of growth during various parts of the growth period. Many details of the growth of the frontal, ethmoid, sphenoid and occipital appear to be shared by modern Homo sapiens and the pongids, although the results relating to the ethmoid and sphenoid suggest there are differences in growth patterns in this region. The results of this study suggest that it is unlikely that any one change in growth mechanism underlies the changes that have occurred during the evolution of hominids from more ape-like ancestors.

The literature review of the soft tissue comparative anatomy of the cranial base has consolidated a great deal of information previously unquoted in studies of fossil and extant primate anatomy. There are some fundamental differences in soft tissue morphology between the pongids and modern Homo sapiens which can be related to the bony architecture of the

cranial base. These observations also assist in the interpretation of many osteological features of the cranial base of fossil hominids.

In the light of these studies, some useful observations can be made about the fossil hominid specimens which have been examined. It appears that cranial base patterns in the fossil taxa are similar to those of the extant taxa and that such patterns can be used to discriminate between the 'gracile' australopithecines on the one hand the the 'robust' australopithecines and early Homo on the other hand. However, because of the similarity between the cranial base pattern of the 'robust' australopithecines and early Homo, the observations made in this study are not useful for distinguishing between the two taxa. Perhaps the most valuable practical result of this thesis for hominid palaeontology is that it has provided an objective method of distinguishing between the cranial base remains of early Homo and those of the 'gracile' australopithecines.

PART V: LITERATURE CITED

LITERATURE CITED

Adams, L.M. and Moore, W.J. (1975) Biomechanical appraisal of some skeletal features associated with head balance and posture in the hominoidea. Acta. anat., 92 : 580-594 .

Aeby, C. (1867) Die schädelformen der menschen und affen. Leipzig.

Arey, L.B. (1949) The craniopharyngeal canal re-interpreted on the basis of its development, (abstract). Anat. Rec., 103 : 420 .

Ashley Montague, M.F. (1943) The mesethmoid-presphenoid relationships in primates. Am. J. phys. Anthropol. 1 : 129-141.

Ashton , E.H. (1957) Age changes in the basicranial axis of the anthropoidea. Proc. zool. Soc., Lond., 129 : 61-74.

Ashton, E.H. and Zuckerman, S. (1951) Some cranial indices of Plesianthropus and other primates. Am. J. phys. Anthropol., 9 : 283-296 .

Ashton, E.H. and Zuckerman, S. (1952a) Age changes in the position of the occipital condyles in the chimpanzee and gorilla. Am. J. phys. Anthropol., 10 : 227-288.

Ashton, E.H. and Zuckerman, S (1952b) The base of the skull in immature hominoids. Am. J. phys. Anthropol., 14 : 611-624.

Ashton, E.H. and Zuckerman, S (1956a) Age changes in the position of the foramen magnum in hominoids. Proc. zool. Soc. Lond., 126 : 315-325.

Ashton, E.H. and Zuckerman, S. (1956b) The base of the skull in immature hominoids. Am. J. phys. Anthropol., 14 : 611-624.

Ashton, E.H. and Spence, T.F. (1958) Age changes in the cranial capacity and foramen magnum of hominoids. Proc. zool. Soc. Lond., 130 : 169-181

Ashton, E.H., Flinn, R.M. and Moore, W.J. (1975) The basicranial axis of certain fossil hominids. J. Zool. Lond., 176 : 577-591.

Baer, K.E. Von (1828) Entwicklungsgeschichte der Thiere : Beobachtung und Reflexion. (Borntträger, Königsberg) 264 pp.

Baer, M.J. (1954) Patterns of growth of the skull as revealed by vital staining. Hum. Biol., 26 : 80-126.

Bassett, C.A.L. (1971) Biophysical principles affecting bone structure. In: The biochemistry and physiology of bone. Bourne, G.H. ed. Second edition. Academic Press, New York.

Bateman, N (1954) Bone growth : A study of the greylethal and microphthalmic mutants of the mouse. J. Anat., 88 : 212-262.

Beer, G.R. de (1962) Embryos and ancestors. 3rd edition. Clarendon Press, Oxford. pp 174.

Biegert, J. (1957) Der formuandel des primatenschädels und seine Beziehungen zur ontogenctischen Entwicklung und den phylogenetischen Spezialisationen der Kopforgane. Morph. Jb. 98 : 77-199 (1957).

Biegert, J. (1963) The evaluation of characteristics of the skull, hands and feet for primate taxonomy. In: classification and human evolution. S.L. Washburn, ed. Aldine : Chicago, pp 116-145.

Björk, A. (1950) Some biological aspects of prognathism and occlusion of the teeth. Acta. odontol. Scandinav., 9 : 1-40.

Björk, A. (1955) Cranial base development. Am. J. Orthod. 41 : 198-225.

Björk, A. and Skieller, V. (1972) Facial development and tooth eruption : An implant study at the age of pubertv. Am. J. Orthod., 62 : 339-383.

Bluntschli, H. (1929) Die kamuskulatur des orang utan und ihro bedentung für die formung des schädels. Morph. Jb. 63 : 531-606.

Bolk, L. (1909) On the position and displacement of the foramen magnum in the Primates. Verk. Akad. Wet. Amst., 12 : 362-377.

Bolk, L. (1910) On the slope of the foramen magnum in primates. Verk. Akad. Wet. Amst. 12 : 525-534.

Bolk, L. (1926) Das problem der menschwierdung. G. Fischer, Jena. 44 pp.

Boyd, T.G., Castelli, W.A. and Huelke, D.F. (1967) Removal of the temporalis muscle from its origin : Effects on the size and shape of the coronoid process. J. Dent. Res., 46 : 997-1001.

Brock, A. and Isaac, G.L.I. (1976) Reversal stratigraphy and its application at East Rudolf. In Y. Coppens, F. Clark Howell, G.L.I. Isaac, and R.E.F. Leakey (eds) : Earliest man and environments in the Lake Rudolf Basin, Chicago : University of Chicago Press, 148-162.

Brodie, A.G. (1941) On the growth pattern of the human head from the third month to the eighth year of life. Am. J. Anat., 68 : 209-262.

Brodie, A.G. (1955) The behaviour of the cranial base and its components as revealed by serial cephalometric roentgenograms. Angle Orthod., 25 : 148-160.

Broom, R. and Schepers, G.W.H. (1946) The South African fossil ape-men The Australopithecinae. Transv. Mus. Mem., 2 : 1-272.

Broom, R., Robinson, J.T. and Schepers, G.W. (1950) Sterkfontein ape-man Plesianthropus. Transv. Mus. Mem., 4 : 1-88.

Broom, R. and Robinson, J.T. (1952) Swartkrans Ape-man. Transv. Mus. Mem., 6 : 1-123.

Bull, J.W.D. (1969) Tentorium cerebelli. Proc. roy. Soc. Med., 62 : 1301-1310.

Butler, H. (1949) A rare suture in the anterior cranial fossa of the human skull. Man : 49 : 25-27.

Cameron, J. (1924) The cranio-facial axis of Huxley. pt. I. Embryological considerations. Trans. r. Soc. Can., 18 : 115-123.

Cameron, J. (1925) The cranio-facial axis of Huxley. pt. II. Comparative anatomy. Trans. r. Soc. Can., 19 : 129-136.

Cameron, J. (1926a) Shortening of the nasion-basion length in the white races. Am. J. phys. Anthropol., 9 : 329-333.

Cameron, J. (1926b) The lengthening of the anterior portion of cranial base in the white races. Am. J. phys. Anthropol., 9 : 338-342.

Cameron, J. (1927) The main angle of cranial base flexion (the nasion-pituitary-basion angle). Am. J. phys. Anthropol., 10 : 275-279.

Cameron, J. (1930) Craniometric memoirs No. II. The human and comparative anatomy of Cameron's craniofacial axis. J. Anat., 64 : 324-336.

Camper, P. (1779) Oeuvres sur l'Histoire Naturelle, en physiologie et l'Anatomie Comparée tomi Anatomie de l'Orang utan. Paris.

Camper, P. (1803) De l'orang-outang, et de quelques autres espèces de singes. In : oeuvres de Pierre Camper qui ont pour objet l'histoire naturelle, le physiologie et l'anatomie comparée, Vol. 1, pp. 5-196, 8°. H.J. Janson (ed.), Paris.

Cave, A.J.E. (1930) The craniopharangeal canal in man and the anthropoids. J. Anat., 65 : 363-367.

Cave, A.J.E. and Haines, R. Wheeler (1940) The paranasal sinuses of the anthropoid apes. J. Anat., 74 : 493-523.

Cave, A.J.E. (1979) The mammalian temporo-pterygoid ligament. J. Zool. Lond., 188 : 517-532.

Champneys, F. (1872) On the muscles and nerves of a chimpanzee (Troglodytes niger) and a Cynocephalus anubis. J. Anat. physiol. Lond. 6 : 176-211.

Clark, W.E. Le Gros (1950) New palaeontological evidence bearing on the evolution of the Hominoidea. Quart. J. geol. Soc. Lond., 105 : 225-264.

Clark, W.E. Le Gros (1971) The antecedents of man (3rd ed.), pp 393. Edinburgh University Press.

Clarke, R.J. (1977) The cranium of the Swartkrans hominid SK 847 and its relevance to human origins. Ph.D. Thesis, University of the Witwatersrand, Johannesburg, South Africa.

Clarke, R.J., Howell, F.C. and Brain, C.K. (1970) More evidence of an advanced hominid at Swartkrans. Nature 225 : 1219-1222.

Clements, E.M.B. and Zuckerman, S. (1953) The order of eruption of the permanent teeth in the Hominoidea. Am. J. phys. Anthropol. 11 : 313-332.

Cousin, R.P. and Fenart, R. (1971) Etude ontogénique des éléments sagittaux de la fosse cérébrale antérieure chez l'Homme orientation vestibulaire. Arch. Anat. Path. 19 : 383-395.

Cramer, D.L. (1977) Craniofacial morphology of Pan paniscus; A morphometric and evolutionary appraisal. Contributions to primatology 10. S. Karger, Basel.

Dart, R.A. (1925) Australopithecus africanus : The man-ape of South Africa. Nature, Lond. 115 : 195-199.

Dart, R.A. (1962) The Makapansgat pink breccia Australopithecine skull. Am. J. phys. Anthropol. 20: 119-126.

Darwin, C. (1859) On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life. J. Murray, London.

Dean, M.C. and Wood, B.A. (1981a) Metrical analysis of the basicranium of extant hominoids and Australopithecus. Am. J. phys. Anthropol. 54 : 63-71.

Dean, M.C. and Wood, B.A. (1981b) Developing pongid dentition and its use for ageing individual crania in comparative cross-sectional growth studies. Folia primatol. 36 : 111-127.

Dörfl, J. (1980a) Migration of tendinous insertions I, cause and mechanism. J. Anat. 131 : 173-178.

Dörfl, J. (1980b) Migration of tendinous insertions II, Experimental modifications. J. Anat. 131 : 229-238.

Downs, W.R. (1952) The role of cephalometrics in orthodontic case analysis. Am. J. Orthod. 38 : 162-182.

Doyle, W.J. and Rood, S.R. (1979) Anatomy of the auditory tube and related structures in the rhesus monkey (macaca milatta). Acta. Anat. 105 : 209-225.

Drake, R.E., Curtis, G.H., Cerling, T.E., Cerling, B.W. and Hampel, J. (1980) KBS Tuff dating and geochronology of tuffaceous sediments in the Koobi Fora and Shungura Formations, East Africa. Nature 283 : 368-372.

DuBrul, E.L. (1950) Posture, locomotion and the skull in Lagomorpha. Am. J. Anat. 87 : 277-313.

DuBrul, E.L. and Laskin, D.M. (1961) Preadaptive potentialities of the mammalian skull : An experiment in growth and form. Am. J. Anat. 109 : 117-132.

DuBrul, E.L. (1977) Early hominid feeding mechanisms. Am. J. phys. Anthropol. 47 : 305-320.

Duckworth, W.L.H. (1904) Studies from the Anthropological Laboratory, The Anatomy School, Cambridge. Cambridge University Press.

Duckworth, W.L.H. (1915) Morphology and anthropology. Second ed., Vol. I. Cambridge University Press, Cambridge.

Dullemeijer, P. (1974) Concepts and approaches in animal morphology. Van Coreum and Co. Assen.

Fenart, R. (1953) Ontogenese cranio-faciale chez l'Homme. Rev. Scient. 91 : 101-115.

Fenart, R. and Deblock, R. (1973) Pan paniscus et Pan troglodytes - craniometrie - Etude comparative et ontogénique selon les méthodes classiques et vestibulaire. Tome 1. Musée Royale de l'Afrique Centrale - Tervuren, Belgique Annales - Serie IN - 8° Sciences Zoologiques - No. 204.

Fisher, J.L., Godfrey, K. and Stephans, R.I. (1976) Experimental strain analysis of infant, adolescent and adult miniature swine skulls subjected to simulated mastication forces. J. Biomech. 9 : 333-338.

Fitch, F.J. and Miller, J.A. (1976) Conventional Potassium Argon and Argon-40/Argon-39 dating of volcanic rocks from East Rudolf. In Y. Coppens, F. Clark Howell, G.L.I. Isaac and R.E.F. Leakey (eds.) : Earliest man and environments in the Lake Rudolf Basin, Chicago : University of Chicago Press, 123-147.

Flower, W.H. and Murie, J. (1867) Account of the dissection of a Bushwoman. J. Anat. Physiol., Lond. 1 : 189-208.

Ford, E.H.R. (1958) Growth of the human cranial base. Am. J. Orthod., 44 : 498-506.

Gavan, J.A. (1953) Growth and development of the chimpanzee : A longitudinal and comparative study. Hum. Biol., 25 : 93-143.

Gavan, J.A. and Swindler, D.R. (1966) Growth rates and phylogeny : in primates. Am. J. phys. Anthropol., 24 : 181-190.

Geoffroy-Saint-Hillaire, I. (1851) Note sur le Gorille. 3rd series. Annales des sciences naturelles, 16 : 154-158.

George, S.L. (1978) A longitudinal and cross-sectional analysis of the growth of the postnatal cranial base angle. Am. J. phys. Anthropol., 49 : 171-178.

Gleadow, A.J.W. (1980) Fission track age of the KBS Tuff and associated hominid remains in northern Kenya. Nature 284 : 225-230.

Gleiser, I. and Hunt, E.E. (1955) The permanent mandibular first molar; its calcification, eruption and decay. Am. J. phys. Anthropol., 13 : 253-284.

Gould, S.J. (1977) Ontogeny and phylogeny. The Belknap press of Harvard University Press, Cambridge, Massachusetts. London, England.

Gould, S.J. (1980) Racism and Recapitulation. Ch. 27, 214-221. In : ever since Darwin : reflections in natural history. Penguin Books.

Gratiolet, C.P. and Alix, P.H.E. (1866) Recherches sur l'anatomie due Troglodytes aubryi, chimpanze d'une espece nouvelle. Nouv. Arch. Mus. Hist. nat., Paris, 2 : 1-264.

Gray, H. (1977) Anatomy, descriptive and surgical. ed. Pick, T.P. and Howden. R. A revised American from the fifteenth English edition. Bounty Books, New York.

Gregory, W.K. (1927) The origin of man from the anthropoid stem - when and where ? Proc. Am. phil. Soc. 66 : 439-463.

Gregory, W.K. (1952) Evolution emerging. New York.

Groth, W. (1937) Vergleichend - anatomische untersuchung Zur Frage der Entslehung des wazenjorsatezes beim menschen und den menschaffen. Morph. Jb. 79 : 358-435.

Grøn, P. (1960) A geometrical evaluation of image size in dental radiography. J. dent. Res., 39 : 289-301.

Haeckel, E. (1866) Generelle morphologie der organismen : Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin feformiste Descendenz-Theorie, 2 vols. (Georg Reisner, Berlin) 574 pp., 462 pp.

Harvey, W. (1645) Exercitatio anatomica de cordis et sanguinis in animalbus. In Adriani Spigelii Anatomica. Amsterdam.

Hill, W.C.O. (1939) Observations on a giant Sumatran Orang. Am. J. phys. Anthropol., 24 : 449-505.

Hillhouse, J.W. Ndombi, J.W.M., Cox, A. and Brock, A. (1977) Additional results on palaeomagnetic stratigraphy of the Koobi Fora Formation, east of Lake Turkana (Lade Rudolf), Kenya. Nature 265 : 411-415.

Hilloowala, R.A. (1969) The laryngeal sacs and air spaces in certain primates. Anat. Rec., 169 : 340 abst.

Holloway, R.L. (1976) Some problems of hominid brain endocast reconstruction, allometry and neural organization. In P.V. Tobias and Y. Coppens (eds.) :Les Plus Anciens Hominides, Paris : CNRS, 69-119.

Holloway, R.L. (1978) Problems of brain endocast interpretation and African hominid evolution. In : C.J. Jolly (ed.) : Early hominids of Africa, Duckworth, London, 379-401.

Howell, F.C. (1978) Hominidae. In : V.J. Maglio and H.B.S. Cooke (eds.) : Evolution of African Mammals, Cambridge : Harvard University Press, 154-248.

Hoyte, D.A.N. and Enlow, D.H. (1966) Wolff's Law and the problem of muscle attachment on resorptive surfaces of bone. Am. J. phys. Anthropol., 24 : 205-213.

Hoyte, D.A.N. (1975) A critical analysis of the growth in length of the cranial base. Birth Defects 11: (7) 255-282.

Hughes, A.R. and Tobias, P.V. (1977) A fossil skull probably of the genus Homo from Sterkfontein, Transvaal. Nature, Lond., 265 : 310-312.

Humphry, G.M. (1867) On some points in the anatomy of the chimpanzee. J. Anat. Physiol., Lond., 1 : 254-268.

Huxley, T.H. (1863) Evidence as to man's place in nature. London : Williams and Norgate, 159 pp.

Huxley, T.H. (1867) On two widely contrasted forms of the human cranium. J. Anat. Physiol., London., 1 : 60-77.

Keith, A. (1910) Description of a new craniometer and of certain age changes in the anthropoid skull. J. Anat. Physiol., Lond., 44 : 251-270.

Klueber, K. and Langdon, H.L. (1979) Anatomy of the musculus levator veli palatini in the 15 week human fetus. Acta. Anat., 105 : 94-105.

Knott, V.B. (1971) Changes in cranial base measurements of human males and females from age 6 to early adulthood. Growth, 35 : 145-158.

Knott, V.B. (1974) Birotundal diameter of the human sphenoid bone from age six years to early adulthood. Am. J. phys. Anthropol., 41 : 279-283.

Koskinen, L. and Koski, K., (1967) Regeneration in transplanted epiphysectomised humeri of rats. Am. J. phys. Anthropol., 27 : 33-40.

Koski, K.L. (1968) Cranial growth centers : Facts or fallacies ? Am. J. Orthod., 54 : 566-583.

Krantz, G.S. (1963) The functional significance of the mastoid processes in man. Am. J. phys. Anthropol., 21 : 591-593.

Krogman, W.M. (1931a,b,c) Studies in growth changes in the skull and face of anthropoids : .

(1931a) Growth changes in the skull and face of the gorilla. Am. J. Anat., 46 : 89-116.

(1931b) Growth changes in the skull and face of the chimpanzee. Am. J. Anat., 47 : 325-342.

1931c) Growth changes in the skull and face of the orang utan. Am. J. Anat., 47 : 343-365.

Kvinnsland, S. (1971) The sagittal growth of the foetal cranial base. Acta. odont. Scand., 29 : 699-715.

Laitman, J.T. (1977) The ontogenetic and phylogenetic development of the upper respiratory system and basicranium in man. PhD. dissertation, Yale University.

Laitman, J.T., Heimbuch, R.C. and Crelin, E.S. (1978) Developmental change in a basicranial line and its relationship to the upper respiratory system in living primates. Am. J. Anat., 152 : 467-483.

Laitman, J.T., Heimbuch, R.C. and Crelin, E.S. (1979) The basicranium of fossil hominids as an indicator of their upper respiratory systems. Am. J. phys. Anthropol., 51 : 15-34.

Latham, R.A. (1972) The sella point and postnatal growth of the cranial base. Am. J. Orthod., 61 : 156-162.

Leakey, R.E.F. (1970) Fauna and artefacts from a new Plio-Pleistocene locality near Lake Rudolf in Kenya. Nature, 226 : 223-224.

Leakey, R.E.F. (1971) Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. Nature 231 : 241-245.

Leakey, R.E.F. (1973) Evidence for an Advanced Plio-Pleistocene hominid from East Rudolf, Kenya. Nature, 242 : 447-450.

Leakey, R.E.F. (1976) An overview of the Hominidae from East Rudolf, Kenya. In Y. Coppens, F. Clark Howell, G.L.I. Isaac and R.E.F. Leakey (eds.) : Earliest man and environments in the Lake Rudolf Basin, Chicago : University of Chicago Press, 490-506.

Leakey, M.D., Clarke, R.J. and Leakey L.S.B. (1971) New hominid skull from Bed I, Olduvai Gorge, Tanzania. Nature 232 : 308-312.

Leakey, R.E.F. Mungai, J.M. and Walker, A.C. (1971) New australopithecines from East Rudolf, Kenya. Am. J. phys. Anthropol., 35 : 175-186.

Leakey, R.E.F. and Mungai, J.M. (1972) New australopithecines from East Rudolf, Kenya (II). Am. J. phys. Anthropol., 36 : 235-251.

Leakey, R.E., Leakey, M.G. and Behrensmeyer, A.K. (1978) The Hominid Catalogue. In : M.G. Leakey and R.E. Leakey (eds.) : Koobi Fora Research Project, Vol. 1 : The fossil hominids and an introduction to their context, 1968-1974. Oxford : Clarendon Press, 86-182.

Leakey, R.E.F. and Walker, A. (1980) On the status of Australopithecus afarensis. Science, 207 : 1103.

Le Double, A.F. (1903) Traite des variations des os crane de l'Homme. Paris.

Lestrel, P.E. and Moore, R.N. (1978) The cranial base in fetal Macaca nemestrinia : A quantitative analysis of size and shape. J. dent. Res., 57 : 395-401.

Lieberman, P. and Crelin, E.S. (1971) On the speech of Neanderthal man. Linguistic Inquiry, 11 : 203-222.

Lightoller, G.S. (1928) The facial muscles of three orang utans and two cercopithecidae. J. Anat., 63 : 19-81.

Løvtrop, S. (1978) Ontogeny and phylogeny. (Reviews), Syst. Zool., 27 : 125-130.

Macalister, A. (1871) On some points in the myology of the chimpanzee and others of the primates. Ann. Mag. Nat. Hist., 7 : 341-351.

Macalister, A. (1873) On the muscular anatomy of the gorilla. R. Irish Acad., 1 : 501-506.

McDougall, I., Maier, R., Sutherland-Hawkes, R. and Gleadow, A.J.W. (1980) K-Ar age estimate for the KBS Tuff, East Turkana, Kenya. Nature 284 : 230-234.

McNeill, R.W. and Newton, G.N. (1965) Cranial base morphology in association with intentional vault deformation. Am. J. phys. Anthropol., 23 : 241-254.

Meckel, J.F. (1811) Entwurf einer Dasstellung der Zwischen dem Embryozustande der höheren tiere und dem permanenten der niederen stattfindenen parallele : Beyträge zur vergleichenden Anatomie, Vol. 2 (Carl Heinrich Reclam, Leipzig)

Michejda, M. (1972) The role of the basicranial synchondrosis in flexure processes and ontogenetic development of the skull base. Am. J. phys Anthropol., 37 : 143-150.

Miller, R.A. (1952) The musculature of Pan paniscus. Am. J. Anat., 91 : 183-232.

Moore, W.J., Adams, L.M. and Lavelle, C.L.B. (1973) Head posture in the hominoidea. J. Zool., Lond., 169 : 409-416.

Moorees, C.F.A., Fanning, E.A. and Hunt, E.E. Jr. (1963) Age variation of formation stages for ten permanent teeth. J. dent. Res., 42 : 1490-1502.

Moss, M.L. (1958) The pathogenesis of artificial cranial deformation. Am. J. phys. Anthropol., 16 : 269-285.

Moss, M.L. (1963) Morphological variations of the crista galli and medial orbital margin. Am. J. phys. Anthropol., 21 : 159-164.

Moss, M.L. (1969) A theoretical analysis of the functional matrix. Acta. Biotheoret., 18 : 195-202.

Moss, M.L. and Young, R.W. (1960) A functional approach to craniology. Am. J. phys. Anthropol., 18 : 281-292.

Moss, M.L. and Meehan, M. (1970) Functional cranial analysis of the coronoid process in the rat. Acta. Anat., 77 : 11-24.

Moss, M.L. (1975) The effect of rombencephalic hypoplasia on posterior cranial base elongation in rodents. Arch. Oral. Biol., 20 : 489-492.

Moss. M.L. and Moss-Salentijn, L. (1978) The muscle bone interface : an analysis of a morphological boundary. In : Fifth symposium on craniofacial growth. ed. D.S. Carbon and J.A. McNamara. Craniofacial growth series, No. 8 39-71. Ann Arber, Univ. of Michigan, Center for Human growth and development.

Murphy, T. (1955) The spheno-ethmoidal articulation in the anterior cranial fossa of the Australian aborigine. Am. J. phys. Anthropol., 13 : 285-300.

Murray, P.D.F. (1936) Bones : A study of the development and structure of the vertebrate skeleton. Cambridge University Press. Cambridge.

Nakamura, S., Savara, B.S. and Thomas, D.R. (1972) Norms of size and angular increments of the sphenoid bone from four to sixteen years. Angle Orthod., 42 : 35-43.

Negus, V.E. (1949) The comparative anatomy and physiology of the larynx. Wm. Heinemann, London.

Olson, T.R. (1978) Hominid phylogenetics and the existence of Homo in Member 1 of the Swartkrans Formation, South Africa. J. Hum. Evol., 7 : 159-178.

Olson, T.R. (1981) Basicranial morphology of the extant hominoids and Pliocene hominids : the new material from the Hadar Formation, Ethiopia, and its significance in early human evolution and taxonomy. In : C.B. Stringer (ed.): Aspects of human evolution. London : Taylor and Francis, 99-128.

Owen, R. (1831) On the anatomy of the orang utan. Proc. zool. Soc., London., 1 : 9, 28-29.

Owen, R. (1835) On the osteology of the chimpanzee and orang. Trans. zool. Soc., Lond., 1 : 343-380.

Owen, R. (1848) On a new species of chimpanzee. (Troglodytes savegei). Proc. zool. Soc., Lond., 16 : 27-35.

Owen, R. (1851) Osteological contributions to the natural history of the chimpanzees (Troglodytes) and orangs (pithecus). No. IV Trans. zool. Soc., Lond., 4 : 75-88.

Parsons, F.G. (1898) The muscles of mammals with special relation to human myology. J. Anat. Physiol., Lond., 32 : 428-450.

Proffitt, W.R., McGlone, R.E. and Barrett, M.J. (1975) Lip and tongue pressures related to dental arch and oral cavity size in Australian aborigines. J. dent. Res., 54 : 1161-1172.

Randall, F.E. (1943) The skeletal and dental development and variability of the gorilla. Hum. Biol., 15 : 307-337.

Rayne, J. and Crawford, G.N.C. (1971) The development of the muscles of mastication in the rat. Ergebn. Anat. Entwickl. Gesch., 44(S) : 1-55.

Raven, H.C. (1950) The Anatomy of the Gorilla. ed. Gregory, W. New York, Columbian University Press.

Robinson, J.T. (1972) The bearing of East Rudolf fossils on early hominid systematics. Nature 240 : 239-240.

Ronning, O. (1966) Observations on the intracerebral transplantation of the mandibular condyle. Acta. odont. Scandinav., 24 : 443-457.

Rowan, R.F. and Turner, L. (1956) The levator palati muscle. J. Anat., 90 : 153-154.

Ruch, T.C. (1941) Bibliographia primatologica. A classified bibliography of primates other than man. Part I. C.C. Thomas, Springfield, Illinois.

Sakka, M. (1977) Ensembles anatomiques Cervice - céphaliques port de tête et évolution des hominides conséquences phylogéniques sur Australopithecus. Mammalia, 41 : 85-109.

Savage, T.S. and Wyman, J. (1847a) Notice of the external characters and habits of Troglodytes gorilla, a new species of orang from the Gaboon river. Proc. Bost. Soc. nat. Hist., 2 : 245-247.

Savage, T.S. and Wyman, J. (1847b) The first scientific identification of the gorilla as a new and hitherto unclassified species of manlike ape. Proc. Bost. Soc. nat. Hist., 5 : 417-443.

Schepers, G.W.H. (1950) The brain casts of the recently discovered Plesianthropus skulls. Part II. Transv. Mus. Mem. No. 4 : 87-117.

Schöneman, A. (1906) Schläfenbein und Schädelbasis, eine anatomisch - otiatrische studie. Nene Denkschr. allg. schweiz. Ges. ges. Naturw., 40 : 90-160.

Schlaginhaufen, O. (1907) Ein Canalis craniopharyngeus persistens an linem menscheuschadel und sein vorkommen bei den anthropoidea. Anat. Anz., 30 : 1-8.

Schour, I. and Massler, M. (1940) Studies in tooth development. J. Am. dent. Assoc., 27 : Part I, 1778-1793 Part II, 1918-1931.

Schluter, F.P. (1976) A comparative study of the temporal bone in three populations of man. Am. J. phys. Anthropol., 44 : 453-468.

Schultz, W. (1917) Der canalis cranio-pharyngeus persistens beim mensch und bei den affen. Morph. Jb. 50 : 417-426.

Schultz, A.H. (1940) Growth and development of the chimpanzee. Carnegie Instit. Wash., Pub. 518. Contrib. Embryol., 28 : 1-63.

Schultz, A.H. (1941) Growth and development of the orang utan. Contrib. Embryol. Carneg. Inst., 29 : 57-111.

Schultz, A.H. (1942) Conditions for balancing the head in primates. Am. J. phys. Anthropol., 29 : 483-497.

Schultz, A.H. (1949) Ontogenetic specializations of man. Archiv. Julius Klaus-Stiftung., 24 : 197-216.

Schultz, A.H. (1955) The position of the occipital condyles and of the face relative to the skull base in primates. Am. J. phys. Anthropol., 13 : 97-120.

Schultz, A.H. (1969) The life of primates. Weidenfeld and Nicolson, London.

Schwartz, D.J. and Huelke, D.F. (1963) Morphology of the head and neck of the macaque monkey : The muscles of mastication and the mandibular division of the trigeminal nerve. J. dent. Res., 42 : 1222-1233.

Scott, J.H. (1953) The variability of cranial and facial dimensions in modern skulls. Brit. dent. J., 95 : 27-31.

Scott, J.H. (1954) Heat regulating function of the nasal mucous membrane. J. Laryn. Otol., 68 : 308-317.

Scott, J.H. (1957) Muscle growth and function in relation to skeletal morphology. Am. J. phys. Anthropol., 15 : 197-233.

Scott, J.H. (1958) The cranial base. Am. J. phys. Anthropol., 16 : 319-348.

Scott, J.H. (1963) Factors determining skull form in primates. In: Symp. zool. Soc., Lond., 10 : 127-135. Ed. Napier, J. and Barnicot, N.A.

Scott, J.H. (1967) Dento-facial development and growth. Pergamon Press.

Serres, E.R.A. (-824) Explication du système nerveux des animaux invertébrés. Ann. Sci. Nat., 3 : 377-380.

Senyurek, M.S. (1938) Cranial equilibrium index. Am. J. phys. Anthropol., 24 : 23-41.

Sergi, S. (1930) Le posizione e la inclinazione del forame occipitale nel cranio neandertaliano di saccopastore. Riv. Anthrop., 29 : 563-657.

Simpson, G.G., Roe, A. and Lewontin, R.C. (1960) Quantitative Zoology (1-440). Harcourt, Brace and World Inc. New York.

Sirianni, J.E. and Vann Ness, A.C. (1978) Postnatal growth of the cranial base in Macaca nemestrina. Am. J. phys. Anthropol., 49 : 329-340.

Skinner, M.F. (1978) Dental maturation, dental attrition and growth of the skull in fossil hominids. Ph.D. Thesis, University of Cambridge.

Sonntag, C.F. (1923) On the anatomy, physiology and pathology of the chimpanzee. Proc. zool. Soc., Lond., : 323-429.

Sonntag, C.F. (1924) The morphology and evolution of the apes and man. J. Bale and Sons. London.

Sperber, G.H. (1976) Craniofacial embryology. Dental practitioner handbook No. 15. Second edition. J. Wright and Sons Ltd., Bristol.

Stark, D. and Kummer, B. (1962) Zur ontogenese des Schimpansens - chadels. (mit Bemerkungen zur fetalistions'ypothese). Anthrop. Anz., 25: 204-215.

Stark, D. (1973) The skull of the fetal chimpanzee (chondrocranium and development of osteocranium). In : The chimpanzee, Vol. 6, pp 1-33. S. Kager, Basel and University Press, Baltimore.

Stamrud, L. (1959) External and internal cranial base : A cross sectional study of growth and of association in form. Acta.odont. Scand., 17 : 239-266.

Swindler, D.R. and Wood, C.D. (1974) An atlas of primate gross anatomy. Baboon, chimpanzee and man. University of Washington Press. Seattle and London.

Takagi, Y., Walters, J.F. and Bosma, J.F. (1962) Anatomical studies of the epipharyngeal wall in relation to the base of the cranium. Ann. Otol. Rhinol. Laryngol., 71 : 366-376.

Talmers, D.A. (1952) Time of eruption of second permanent molar and relationship to body size and areolar development. Preliminary report. N.Y. St. dent. J., 18 : 314-315.

Tanner, J.M. (1962) Growth at adolescence : With a general consideration of the effects of hereditary and environmental factors upon growth and maturation from birth to maturity. (end ed.) Blackwell Scientific Publications, Oxford.

Taxman, R.M. (1963) Incidence and size of the juxtamastoid eminence in modern crania. Am. J. phys. Anthropol., 21 : 153-157.

Tobias, P.V. (1967) Olduvai Gorge, Vol. 2., The cranium and maxillary dentition of Australopithecus (Zinjanthropus) boisei. Cambridge University Press, Cambridge.

Tobias, P.V. (1978) The South African australopithecines in time and hominid phylogeny, with special reference to the dating and affinities of the Taung skull. In : Early hominids of Africa. C.J. Jolly (ed.) Duckworth, London, pp. 45-84.

Tobias, P.V. (1980) The natural history of the helicoidal occlusal plane and its evolution in early Homo. Am. J. phys. Anthropol., 53 : 173-187.

Tobias, P.V. (1981) A survey and synthesis of the African hominids of the late Tertiary and early Quaternary periods. In : L.K. Königgson (ed.) : Current Argument on Early Man. Oxford : Pergamon Press , 86-113.

Topinard, P. (1890) Anthropology. Chapman and Hall, London.

Townsley, W. (1948) The influence of mechanical factors on the development and structure of bone. Am. J. phys. Anthropol., 6 : 25-45.

Turnbull, W.D. (1978) Another look at dental specialization in the extinct sabre-toothed marsupial Thylacosmilus, compared with its placental counterparts. In : Development function and evolution of teeth. (ed.) Butler, P.M. and Joysey, E.A. Academic Press, pp. 399-414.

Tyson, E. (1699) Orang-Outang Sive Homo Sylvestris; or the anatomy of a pygmie compared with that of a Monkey an Ape and a Man. To which is added a philological essay concerning the pygmies, the cynocephali, the sattyrs and sphinges of the ancients. T. Bennet. London.

Vesalius, A. (1543) De Corporis Humani Fabrica. Padua.

Virchow, R. (1857) Untersuchungen über die Entwiskelung des Shädelgrundes im gesunden und Krnakhaften Zustande und über den Einfluss desselben auf Schädelform Gesüchtsbildung und Gehirnban, 6 Tafeln. G. Riemer, Berlin.

Walensky, N.A. (1964) A re-evaluation of the mastoid region of contemporary and fossil man. Anat. Rec., 149 : 67-72.

Walker, A. (1976) Remains attributable to Australopithecus in the East Rudolf Basin, Chicago. : University of Chicago Press, 484-489.

Washburn, S.L. (1947) The relation of the temporal muscle to the form of the skull. Anat. Rec., 99 : 239-248.

Washburn, S.L. and Clark Howell, F. (1952) On the identification of the hypophysial fossa of solo man. Am. J. phys. Anthropol., 10 : 13-21.

Weidenreich, F. (1941) The brain and its role in the phylogenetic transformation of the human skull. Trans. Am. phil. Soc., 31 : 321-442.

Weidenreich, F. (1943) The skull of Sinanthropus pekinensis : A comparative study on a primitive hominid skull. Paleont. Sinica. New Ser. D, No. 10, whole ser. No. 127, pp. 1-134.

Weidenreich, F. (1947) Some particulars of skull and brain of early hominids and their bearing on the problem of the relationship between man and anthropoids. Am. J. phys. Anthropol., 5 : 387-428.

Weidenreich, F. (1951) Morphology of solo man, 43 : Part 3. Anthropological papers of the American Museum of Natural History New York : 205-290.

Wilder, B.G. (1861) Contributions to the comparative myology of the chimpanzee. Boston J. nat. Hist., 7 : 353-384.

Willoughby, D.P. (1978) All about Gorillas. A.S. Barnes and Co., New Jersey.

Wind, J. (1970) On the phylogeny and the ontogeny of the human larynx. Wolters-Woordhoff publishing, Gronigen.

Wind, J. (1978) Fossil evidence for primate vocalizations ? In : Recent advances in primatology, Vol. 3 : 87-91. (ed.) Chivers, D.J. and Joysey, K.A., Academic Press.

Wolff, J. (1892) Das Gesetz der Transformation der knochen. Berlin.

Wolpoff, M.H. (1970) The evidence for multiple hominid taxa at Swartkrans. Am. Anthrop., 72 : 576-607.

Wolpoff, M.H. (1971) Is the new composite cranium from Swartkrans a small robust australopithecine ? Nature, 230 : 398-401.

Wolpoff, M.H. (1974) The evidence for two australopithecine lineages in South Africa. Yb. Phys. Anthropol., 17 : 113-139.

Wolpoff, M.H. (1978a) Analogies and interpretation in palaeoanthropology. In : C.J. Jolly (ed.) : Early hominids of Africa. London : Duckworth, 461-503.

Wolpoff, M.H. (1978b) Some aspects of canine size in the australopithecines. J. Hum. Evol., 7 : 115-126.

Wood, B.A. (1976) Remains attributable to Homo in the East Rudolf succession. In : Y. Coppens, F. Clark Howell, G.L.I. Isaac and R.E.F. Leakey (eds.) : Earliest man and environments in the Lake Rudolf Basin, Chicago : University of Chicago Press, 490-506.

Wood, B.A. (1978) Classification and phylogeny of East African hominids. In: D.J. Chivers and K.A. Joysey (eds.) : Recent Advances in Primatology, Vol. 3, London. Academic Press, 351-372.

Wood Jones, F. (1923) The ancestry of man, Brisbane.

Wood Jones, F. (1929a) Man's place among the mammals. E. Arnold, London.

Wood Jones, F. (1929b) Some landmarks in the phylogeny of the primates. Hum. Biol., 1 : 214-228.

Wyman, J. (1855) An account of the dissection of a black chimpanzee (Troglodytes niger) : A comparison of the muscular system of Troglodytes with that of man. Proc. Bost. Soc. nat. Hist., 5 : 274-276.

Young, M. (1916) A contribution to the study of the Scottish skull. Trans. R. Soc., Edin., 51 : 347-454.

Zuckerman, S. (1955) Age changes in the basicranial axis of the human skull. Am. J. phys. Anthropol., 13 : 521-539.

Zuckerman, S., Ashton, E.H. and Pearson, J.B. (1962) The styloid of the primate skull. Bibl. primat., 1 : 217-228. (S. Karger, Basel).

PART VI. APPENDIX

APPENDIX

Data for each individual specimen included in this thesis were set out on two computer cards, the number of which appears in Column 1 of the computer print out. Column 2 is a taxon code; (Homo = 0, Pan = 2, Gorilla = 4, Pongo = 6, and the fossil hominids = 8). The specimens within each taxon are numbered 1 - 30 for the adults and from 31 onwards for the juveniles in decreasing relative dental age, beginning with the oldest juvenile specimen (No. 31). The specimen number appears in Columns 3 and 4. Where sex is known for any of the specimens, it is included and appears in Column 5 (♂ = 1, ♀ = 2). The juvenile or adult status of an individual appears in Column 6 (2 = adult, 1 = juvenile). All the variables recorded in this thesis, including measurements from radiographs and the % magnification values used to correct certain values, appear in the appendix. The corresponding card number and column number for each variable is indicated by the key at the top of each page. When a specimen has an index or catalogue number, this appears in the last column of Card 1 for that specimen.

CARD 2.

CARD 1.

CARD NO.	TAXON NO.	SPECIMEN NO.	SEX	JUVENILE/ADULT	CC-TP RDA	MAX W. α	X RAY W. β	% DIST. W. IT-IT/TP-TP	MAX L. Fo-Fo/TP-TP	X RAY L. IT-IT/BS % DIST. L. γ	IT-IT MO-MO	Fo-Fo OC-OC	CC-CC SOF-SOF	PA-PA PT-PT	TP-TP IT-HA	FM-FM NA-FC	BS-OP FC-CL	SP-SP CR-CR	SM-SM FC-PS	SB-BS PS-SB	CC-PA
HOMO ADULT	1001	2	40								77	51	55	31	102	31	39	72	80	26	21
	2001	2	24	55	107	50	22	53													
	1002	2	40								64	47	55	34	98	29	33	77	80	25	17
	2002	2	21	55	105	45	26	46													
	1003	2	40								71	54	63	36	105	30	35	80	85	26	23
	2003	2	21	47	102	47	28	45													
	1004	2	40								68	49	54	32	100	32	35	76	80	27	17
	2004	2	25	44	104	52	27	49													
	1005	2	40								69	49	56	36	104	28	35	80	83	28	16
	2005	2	23	43	108	42	26	43													
	1006	2	40								66	49	51	30	97	30	34	75	79	25	18
	2006	2	26	50	102	47	27	48													
	1007	2	40								74	56	61	38	108	27	33	86	91	27	15
	2007	2	26	46	109	48	22	47													
	1008	2	40								64	47	52	29	97	25	34	80	81	26	14
	2008	2	23	46	110	43	27	44													
	1009	2	40								61	45	53	30	92	30	33	75	73	27	16
	2009	2	19	45	106	54	26	52													
	1010	2	40								68	52	57	32	100	31	36	79	83	27	19
	2010	2	22	51	106	45	27	42													
	1011	2	40								59	45	56	27	97	33	35	73	79	26	22
	2011	2	22	48	107	43	22	40													
	1012	2	40								66	51	60	33	100	27	35	80	85	28	22
	2012	2	23	48	108	43	26	45													
	1013	2	40								64	54	60	32	103	31	39	83	87	31	23
	2013	2	24	52	103	41	23	40													
	1014	2	40								65	50	57	32	92	30	32	77	78	27	18
	2014	2	20	44	108	43	26	44													
	1015	2	40								68	50	60	36	102	29	39	81	87	30	19
	2015	2	23	42	102	55	29	51													
	1016	2	40								71	53	58	29	103	30	35	76	81	20	17
	2016	2	22	31	112	49	28	48													
	1017	2	40								63	51	56	30	96	29	33	74	80	24	18
	2017	2	20	39	106	53	28	50													
	1018	2	40								67	49	55	33	96	32	40	77	80	26	16
	2018	2	20	40	106	47	24	46													
	1019	2	40								61	45	54	28	95	31	36	73	76	21	19
	2019	2	18	47	107	50	24	47													
	1020	2	40								60	50	59	31	101	27	29	72	80	24	20
	2020	2	22	49	106	53	24	52													
	1021	2	40								68	48	51	31	99	27	37	78	79	29	19
	2021	2	25	55	106	45	26	42													
	1022	2	40								70	51	62	38	100	34	37	87	91	28	18
	2022	2	20	46	109	52	32	48													
	1023	2	40								68	45	61	32	101	31	36	79	84	22	21
	2023	2	15	46	109	47	25	48													
	1024	2	40								66	51	62	29	100	31	40	85	88	20	22
	2024	2	20	43	112	49	27	50													
	1025	2	40								67	50	56	29	100	32	40	77	79	25	18
	2025	2	17	44	107	47	24	48													
	1026	2	40								65	49	56	33	96	27	32	77	79	27	18
	2026	2	24	53	109	52	24	48													
	1027	2	40								57	50	61	38	99	30	35	79	83	21	16
	2027	2	24	41	111	45	24	48													
	1028	2	40								58	45	54	27	97	31	33	73	76	22	18
	2028	2	19	48	112	53	26	42													
	1029	2	40								68	50	59	39	103	30	38	82	85	28	18
	2029	2	18	42	113	50	32	52													
	1030	2	40								63	51	54	32	95	29	33	75	78	24	18
	2030	2	21	39	102	47	25	47													
HOMO JUVENILE	1031	1	380								60	50	58	32	97	26	34	80	83	24	18
	2031	1	23	47	106	50	28	49													
	1032	1	370								62	48	57	29	95	21	33	82	87	21	20
	2032	1	20	48	103	47	22	44													
	1035	1	360								59	45	55	30	94	28	34	74	76	23	19
	2033	1	20	45	105	42	21	44													

CARD 2.

CARD 1.

CARD NO. / TAXON NO.	SPECIMEN No.	SEX	JUVENILE / ADULT	RDA	CC-TP	MAX W. α	X RAY W. β	% DIST. W. IT-IT/TP-TP	MAX L. FO-FO/TP-TP	X RAY L. IT-IT / BS	% DIST. L. γ	IT-IT	MO-MO	FO-FO	OC-OC	CC-CC	SOF-SOF	PA-PA	PT-PT	TP-TP	IT-HA	FM-FM	NA-FC	BS-OP	FC-CL	SP-SP	CR-CR	SM-SM	FC-PS	SB-BS	PS-SB	CC-PA
1034	1			320								58	49	54	26	84	27	30	69	69	20	16
2034	1			18	40	110	40	26	40																							
1035	1			290								64	50	59	28	102	28	35	79	81	24	22
2035	1			24	40	105	45	20	45																							
1036	1			280								66	50	59	28	95	28	35	80	84	23	21
2036	1			21	45	107	46	25	45																							
1037	1			280								65	47	58	29	95	29	37	83	87	22	20
2037	1			21	40	105	50	28	40																							
1038	1			260								58	44	56	32	97	31	36	78	82	23	17
2038	1			23	45	100	43	29	43																							
1039	1			240								61	48	53	27	95	26	35	73	77	19	20
2039	1			23	48	115	48	29	38																							
1040	1			230								59	50	57	32	92	32	35	77	81	19	18
2040	1			19	40	100	45	20	46																							
1041	1			210								62	53	61	32	100	32	38	75	78	22	19
2041	1			21	35	99	44	26	47																							
1042	1			200								56	42	52	29	95	28	32	74	79	23	17
2042	1			21	40	102	43	26	40																							
1043	1			200								62	47	56	25	92	32	37	78	82	20	20
2043	1			17	38	100	43	20	46																							
1044	1			190								56	43	60	26	90	27	31	68	72	20	20
2044	1			22	45	105	44	27	35																							
1045	1			180								58	48	53	26	89	28	34	73	78	20	17
2045	1			20	40	106	48	26	46																							
1046	1			160								56	44	48	23	84	25	28	67	71	17	17
2046	1			21	49	108	39	23	35																							
1047	1			160								65	48	46	33	91	31	35	78	80	19	15
2047	1			20	35	105	45	23	45																							
1048	1			150								57	48	56	28	92	27	31	74	83	20	21
2048	1			19	39	100	44	26	44																							
1049	1			140								60	45	48	28	90	28	33	72	79	18	16
2049	1			21	45	110	44	23	47																							
1050	1			140								57	47	55	27	92	30	35	76	79	22	19
2050	1			19	35	108	38	21	36																							
1051	1			130								54	43	53	27	83	30	33	74	80	20	17
2051	1			17	44	110	39	22	39																							
1052	1			120								56	45	51	28	85	31	34	72	75	15	13
2052	1			19	30	108	41	23	39																							
1053	1			120								58	44	48	25	83	27	32	67	68	17	15
2053	1			18	40	105	39	22	38																							
1054	1			115								56	43	50	24	79	27	34	68	72	16	15
2054	1			17	33	106	36	17	36																							
1055	1			115								58	49	57	25	95	23	34	78	83	19	22
2055	1			20	35	100	44	28	46																							
1056	1			100								58	42	52	29	79	24	27	74	75	24	17
2056	1			15	48	96	36	24	40																							
1057	1			100								56	44	51	26	86	28	35	71	73	17	16
2057	1			17	43	106	38	23	33																							
1058	1			100								58	46	53	25	84	28	34	73	76	19	17
2058	1			17	35	110	38	21	37																							
1059	1			100								49	42	46	25	74	27	32	68	70	16	13
2059	1			15	40	100	35	15	39																							
1060	1			100								49	46	47	22	74	22	32	62	65	16	14
2060	1			16	35	105	38	20	41																							
1061	1			90								52	45	48	22	75	23	30	60	65	21	13
2061	1			20	45	110	40	21	39																							
1062	1			90								50	46	59	26	92	33	38	82	84	18	20
2062	1			19	37	105	45	27	43																							
1063	1			85								54	43	47	23	75	25	29	65	70	21	15
2063	1			15	34	103	39	19	37																							
1064	1			80								59	42	50	24	80	27	30	69	72	15	17
2064	1			18	34	110	39	26	35																							
1065	1			70								52	41	48	20	80	29	33	71	76	19	19
2065	1			17	40	105	40	24	37																							
1066	1			60								50	40	45	23	78	24	38	66	70	19	16
2066	1			16	40	109	36	23	36																							

CARD 2.

CARD 1.

CARD NO. / TAXON NO. / SPECIMEN No. / SEX / JUVENILE/ADULT	CC-TP	RDA	MAX W. α	X RAY W. β	% DIST. W. IT-IT/TP-TP	MAX L. FO-FO/TP-TP	X RAY L. IT-IT / BS	% DIST. L. γ	IT-IT	FO-FO	CC-CC	PA-PA	TP-TP	FM-FM	BS-OP	SP-SP	SM-SM	SB-BS	CC-PA	
1067 1		50							53	42	44	22	72	27	31	63	67	16	14	
2067 1	16	37	105	35	20	36														
1068 1		50							53	41	54	22	83	29	30	72	75	16	18	
2068 1	17	35	105	39	19	39														
1069 1		40							47	36	42	21	69	24	29	59	62	14	15	
2069 1	15	42	103	32	18	32														
1070 1		40							51	43	45	22	71	23	29	62	65	17	15	
2070 1	14	44	106	35	19	33														
1071 1		40							50	39	43	20	69	23	29	61	64	16	17	
2071 1	14	47	94	35	15	36														
1072 1		40							52	43	49	22	71	26	33	67	70	16	17	
2072 1	17	45	100	35	22	34														
1073 1		30							50	42	45	20	69	25	31	63	66	15	15	
2073 1	13	34	105	35	19	35														
1074 1		20							48	38	43	20	69	25	27	62	65	15	16	
2074 1	14	45	105	34	20	34														
1075 1		20							52	40	39	23	66			57	61		12	
2075 1	14	48	92	29	13															
1076 1		15							46	34	37	18	61	23	26	56	60	17	14	
2076 1	13	43	103	30	15	37														
1077 1		10							42	36	36	14	50	20	23	54	56	14	15	
2077 1	8	40	98	28	13	15														
1078 1		05							41	32	30	14	38	16	20	38	45	15	17	
2078 1	5	55	90	21	11	28														
1079 1		05							43	33	30	18	38	16	21	36	44	15	13	
2079 1	5	46	115	20	12	29														
1080 1		05							43	31	29	14	36	16	20	31	36	14	12	
2080 1	2	45	110	19	10	28														
PAN ADULT																				
120122	22	109	113	4	165	178	8		46	40	38	21	98	21	29	63	65	22	22	1939 5367
220122	30	64	93	44	23	45	155		17	22	32	60	25	22	170	57	21	25		
120222	22	122	128	5	184	198	8		48	39	44	25	104	24	24	57	64	26	25	1939 3369
220222	29	69	92	43	24	48	155		21	25	39	64	27	20	150	66	23	21		
120312	22	130	137	5	199	215	8		50	45	40	22	108	20	27	52	58	25	21	1968 758
220312	35	67	105	52	24	53	160		22	26	37	68	24	19	162	93	21	26		
120412	22	123	129	5	181	195	8		50	47	43	24	104	24	28	60	64	26	26	64.12.16
220412	31	69	95	44	26	44	155		18	25	34	69	28	22	134	60	29	22		
120512	22	123	128	4	188	206	10		50	45	44	22	105	24	31	63	67	25	23	87.12.2.1
220512	32	65	91	46	25	49	160		16	25	35	68	22	20	148	98	26	26		
120612	22	119	123	3	188	206	10		50	43	43	27	104	22	25	62	66	28	23	1939 3384
220612	33	72	98	50	26	54	156		20	25	44	66	25	19	160	70	28	24		
120722	22	118	123	4	184	205	11		52	39	43	25	105	22	25	58	63	27	27	88.12.8.18
220722	33	75	90	48	21	58	153		19	24	35	69	30	22	164	68	28	24		
120812	22	128	135	6	191	210	10		52	43	44	23	110	22	29	58	67	24	26	1939.3365
220812	33	70	103	55	30	53	150		18	23	30	70	29	24	142	76	29	27		
120912	22	123	130	6	181	197	9		50	43	40	23	103	22	27	55	58	28	23	1968 575
220912	32	71	98	46	26	50	156		19	22	32	68	30	22	146	87	25	22		
121012	22	135	141	4	200	220	10		53	44	47	27	118	23	27	64	68	28	26	87.12.12
221012	35	71	102	56	27	57	158		20	26	42	73	30	22	162	70	31	25		
121112	22	133	140	5	192	219	14		52	44	43	25	112	22	25	62	66	31	22	2A
221112	34	68	101	50	27	53	160		20	25	38	65	27	25	162	76	29	22		
121212	22	130	136	5	195	212	9		51	45	48	23	104	23	27	60	61	27	24	17.12.16.1
221212	34	55	94	47	23	52	165		21	28	34	70	28	24	166	114	29	23		
121322	22	120	126	5	180	195	8		50	43	42	23	105	28	30	62	63	26	22	20.4.13.2
221322	32	66	91	46	19	52	155		13	22	34	65	25	15	130	74	26	27		
121422	22	116	120	3	173	189	9		45	37	38	23	90	20	22	63	65	22	21	1939 3366
221422	26	69	100	52	27	51	143		22	24	30	66	21	22	148	62	24	30		
121512	22	123	127	3	200	223	12		49	44	40	25	98	24	29	55	58	28	22	18-9-10
221512	34	72	99	48	22	51	160		20	29	43	69	23	24	174	58	27	25		
121622	22	124	129	4	191	219	15		53	45	41	25	102	21	27	54	61	25	25	1939 3382
221622	30	70	94	56	27	57	167		23	30	42	75	25	30	178	62	19	29		
121712	22	122	128	5	189	205	9		50	42	43	26	104	23	32	62	66	27	22	1939 3377
221712	31	76	94	42	27	41	165		19	24	31	62	25	14	158	78	31	22		
121812	22	131	138	5	200	227	13		53	48	40	25	110	25	32	54	59	28	20	64.12.17
221812	34	72	102	54	27	57	163		19	25	40	67	28	17	178	63	28	20		
121922	22	118	122	3	179	193	8		50	42	41	27	94	22	26	66	69	26	25	1939 3370
221922	26	78	98	48	25	50	151		19	26	39	67	25	14	142	65	31	19		

CARD2.

CARD1.

CARD NO. TAXON NO. SPECIMEN NO. SEX JUVENILE/ADULT	CC-TP	RDA	MAX W. α	X RAY W. β	% DIST. W. IT-IT/TP-TP	MAX L. Fo-Fo/TP-TP	X RAY L. IT-IT/BS	% DIST. L. γ	IT-IT	Fo-Fo	CC-CC	PA-PA	TP-TP	FM-FM	BS-OP	SP-SP	SM-SM	SB-BS	CC-PA	
122012	22	140	146	4	200	206	3	57	45	47	28	115	26	32	61	63	29	29	1968 751
222012	34	72	98	56	32	54	152	22	28	39	75	30	20	146	98	34	25		
122112	22	125	136	9	208	214	3	42	38	41	20	108	22	28	63	68	27	25	1939 3363
222112	36	70	95	52	25	55	161	21	26	37	65	32	24	168	94	24	22		
122212	22	135	141	4	198	217	10	50	42	45	21	113	23	29	57	61	30	27	1922.12.19.1
222212	36	71	90	44	19	51	158	20	26	34	71	30	22	144	74	26	26		
122312	22	135	140	4	200	207	4	52	43	48	28	112	27	34	60	61	28	26	7.7.8.19
222312	35	71	101	53	29	51	168	23	28	37	68	29	22	147	68	31	23		
122412	22	132	139	5	202	212	5	55	42	40	28	108	23	28	55	58	28	23	1939.3364
222412	32	76	95	48	22	52	155	26	31	37	70	27	23	170	75	32	25		
122522	22	123	132	7	199	210	6	59	45	44	25	107	25	28	60	66	24	20	M706
222522	31	60	94	48	29	56	158	23	27	42	73	28	22	165	70	26	26		
122622	22	112	121	8	176	193	10	50	40	43	20	95	25	26	54	58	20	26	M506(3)
222622	27	62	91	47	21	53	155	19	21	37	66	28	21	155	88	28	22		
122722	22	118	126	7	193	213	10	55	46	45	20	100	26	31	64	69	28	26	M506
222722	28	59	92	48	25	54	150	21	27	43	69	25	17	170	80	28	26		
122822	22	118	127	8	187	207	11	51	45	39	24	104	24	33	63	65	26	26	M720
222822	32	75	90	45	24	52	150	22	25	39	65	30	23	170	92	24	25		
122922	22	130	139	7	204	213	4	55	46	43	26	109	24	31	63	67	28	25	M677
222922	27	66	103	52	27	52	150	23	26	40	70	31	18	175	104	26	24		
123022	22	112	126	13	184	203	10	51	39	40	22	92	25	27	58	65	24	24	M676
223022	33	67	86	43	21	50	150	21	24	40	72	25	17	162	68	26	23		
DAN 1231 1	18	105	115	10	176	192	9	49	38	41	19	98	24	33	62	65	23	24	1939 3386
JUVENILE 2231 1	29	66	95	48	25	47	155	15	23	42	70	23	17	175	74	28	25		
1232 1	178	122	131	7	185	200	8	53	42	45	21	115	28	27	62	68	27	25	1939 3373
2232 1	35	65	93	49	23	50	155	16	26	43	70	25	17	170	105	21	24		
1233 1	175	117	127	9	178	194	9	48	41	40	21	102	26	31	58	63	27	23	1939 908
2233 1	30	66	88	48	20	55	152	13	25	40	66	24	22	200	94	29	28		
1234 1	170	107	112	5	176	190	8	47	42	42	21	98	25	28	61	64	25	29	C372
2234 1	24	65	93	45	23	45	158	13	21	31	65	23	22	175	76	29	26		
1235 1	160	112	122	9	172	191	11	50	43	42	20	103	27	30	56	63	23	25	77818
2235 1	29	65	91	50	28	52	154	15	23	37	68	17	14	189	75	29	28		
1236 1	157	116	123	6	173	193	12	51	48	45	24	112	24	26	66	68	24	22	M 52
2236 1	29	67	92	44	20	52	154	14	22	32	69	23	11	150	80	25	28		
1237 1	156	110	119	8	166	185	11	49	42	32	21	95	22	35	53	57	24	28	M455
2237 1	24	72	90	47	19	51	150	14	22	37	66	19	20	170	84	26	28		
1238 1	152	115	124	8	160	175	9	48	41	33	18	83	22	31	51	57	22	21	C370
2238 1	27	73	95	47	19	51	150	14	21	33	67	20	17	165	80	25	21		
1239 1	146	116	120	3	180	195	8	49	43	43	21	91	21	26	55	59	22	22	M371
2239 1	24	67	90	42	20	49	149	14	20	39	70	22	14	172	82	24	20		
1240 1	135	103	114	11	164	174	6	47	40	38	21	82	20	31	57	60	20	22	1939 3387
2240 1	20	72	93	41	22	43	158	14	20	37	63	20	17	170	75	25	21		
1241 1	130	111	120	8	178	195	10	52	43	41	24	98	24	32	62	64	25	23	R5
2241 1	27	68	89	44	20	49	149	17	24	33	72	21	13	170	90	28	26		
1242 1	128	110	118	7	171	188	10	54	46	41	21	108	25	28	65	68	25	23	M573
2242 1	30	66	93	42	20	49	155	17	26	41	68	21	16	164	84	27	24		
1243 1	128	108	111	3	164	175	7	42	39	47	25	93	23	27	57	59	17	22	M891
2243 1	27	73	90	42	22	46	148	14	21	32	64	20	15	168	80	22	22		
1244 1	128	103	110	7	164	180	10	46	41	43	20	92	24	33	57	61	21	21	M636
2244 1	23	57	88	40	22	46	143	11	20	32	64	20	16	155	78	23	23		
1245 1	127	116	125	8	176	197	12	51		39	71	104	26	33	62	64	24	21	M454
2245 1	23	67	89	36	22	49	142	17	24	41	68	21	15	165	100	25	25		
1246 1	126	112	119	6	176	192	9	52	43	43	24	97	26	31	61	66	22	24	2 IV 35
2246 1	29	64	94	45	25	46	150	17	25	35	71	23	18	162	100	23	27		
1247 1	126	104	108	4	163	172	6	45	36	36	19	87	22	33	54	56	18	22	M382
2247 1	22	68	95	41	21	42	150	14	20	35	73	22	13	172	99	24	24		
1248 1	125	111	114	3	158	176	11	47	41	34	20	87	24	29	57	59	20	20	M363
2248 1	16	62	93	42	26	46	148	14	18	28	66	21	17	160	75	23	21		
1249 1	125	110	116	5	162	185	14	47	38	38	20	91	23	30	56	61	21	23	M746
2249 1	24	65	96	44	25	44	151	13	21	41	64	20	13	190	104	23	22		
1250 1	125	106	109	3	151	167	11	50	35	39	19	83	21	25	55	56	21	22	M274
2250 1	24	71	90	40	20	43	155	13	21	33	65	24	15	158	50	23	20		
1251 1	125	110	118	7	165	178	8	47	39	42	24	94	23	29	57	63	23	24	M170
2251 1	27	68	85	42	22	47	151	12	21	36	66	21	18	175	84	23	22		

CARD2.

CARD1.

CARD NO.	TAXON NO.	SPECIMEN NO.	SEX	JUVENILE/ADULT	RDA	CC-TP	MAX W.	X RAY W.	% DIST. W.	IT-IT/TP-TP α	MAX L.	X RAY L.	% DIST. L.	FO-AO/TP-TP β	IT-IT/BS γ	IT-IT	MO-MO	FO-FO	OC-OC	CC-CC	SOF-SOF	PA-PA	PT-PT	TP-TP	IT-HA	FM-FM	NA-FC	BS-OP	FC-CL	SP-SP	CR-CR	SM-SM	FC-PS	SB-BS	PS-SB	CC-PA	
1252	1		124	97	105	9	166	177	7							47		37		41		19	86	22	31		51		57	23	19	1899
2252	1		25	67	102	41	22	40	149							10		21		32		69	21	12	170		83		22	20		
1253	1		124	106	109	3	155	170	10							47		37		36		19	91	23	26		57		60	22	21	M805
2253	1		25	65	90	45	23	48	147							15		21		34		64	21	18	152		50		25	25		
1254	1		123	109	115	6	159	172	8							49		40		40		16	96	23	29		55		59	19	23	M 851
2254	1		16	69	94	40	20	44	147							13		22		32		70	21	16	177		80		23	22		
1255	1		122	107	110	3	163	176	8							49		42		37		22	95	22	27		56		58	22	21	M 801
2255	1		25	67	90	43	25	47	158							14		21		39		71	20	15	192		94		19	25		
1256	1		120	113	120	6	183	203	11							52		45		41		20	103	22	32		57		64	23	24	5558
2256	1		30	65	93	46	23	48	150							19		23		36		75	19	15	177		94		27	21		
1257	1		119	105	114	9	171	184	8							51		38		40		23	98	24	31		59		62	23	22	26.11.19.1
2257	1		30	67	90	40	21	46	149							19		24		38		70	17	15	150		78		22	27		
1258	1		119	106	113	7	157	175	11							48		39		41		18	85	20	27		54		59	19	22	M118
2258	1		22	61	97	41	22	38	151							14		21		34		68	20	22	187		64		21	18		
1259	1		114	101	111	10	154	165	7							49		40		35		20	90	23	31		55		58	19	20	C195
2259	1		25	67	97	45	25	41	150							13		21		30		67	23	11	195		75		22	24		
1260	1		114	109	117	7	163	182	12							51		41		42		25	92	24	27		56		59	19	21	M145
2260	1		26	60	90	40	18	43	145							13		20		35		69	20	20	170		78		25	24		
1261	1		114	106	114	8	167	182	9							51		40		36		20	91	25	31		54		58	23	24	M259
2261	1		27	59	93	45	24	47	150							20		24		38		71	21	14	160		70		27	23		
1262	1		113	102	108	6	156	176	13							46		37		37		20	87	24	27		53		57	21	23	M 94
2262	1		26	69	89	40	22	46	150							14		20		30		63	18	11	160		94		30	27		
1263	1		113	102	107	5	163	177	9							47		42		43		20	92	23	30		54		58	19	19	39.3372
2263	1		26	73	85	44	25	44	150							12		21		31		70	18	16	186		50		22	22		
1264	1		112	104	110	6	150	165	10							47		41		42		25	88	27	31		59		63	20	20	M 358
2264	1		24	68	100	43	24	42	150							11		19		38		70	23	12	160		68		20	24		
1265	1		111	97	103	6	153	167	9							42		37		39		20	85	24	29		53		57	19	22	M 507
2265	1		32	67	88	35	17	40	150							10		17		31		65	20	10	150		81		22	22		
1266	1		110	101	109	8	158	171	8							51		37		38		20	91	23	29		55		59	20	21	39.99.82
2266	1		26	67	95	40	23	42	155							15				35		72	16	17	180		94		20	24		
1267	1		107	107	111	4	160	174	9							51		36		41		22	79	21	29		52		55	17	22	M675
2267	1		21	68	94	37	20	39	145							11		17		27		62	17	15	160		65		18	22		
1268	1		107	101	106	5	154	166	8							45		38		38		18	82	26	30		56		60	20	22	1939 3371
2268	1		25	60	90	37	20	41	145							7		21		30		65	16	14	168		110		20	25		
1269	1		105	101	109	8	165	178	8							46		34		34		17	89	23	29		55		57	21	20	1939.3381
2269	1		28	67	95	43	23	47	154							11		19		37		66		12	144		88		22	22		
1270	1		102	98	102	4	155	170	10							47		36		35		16	82	23	31		55		56	20	21	18911
2270	1		23	64	93	40	26	40	150							10		21		37		65	26	12	153		70		22	22		
1271	1		104	97	101	4	151	163	8							47		39		35		19	83	22	28		51		55	15	25	1934 1003
2271	1		17	66	90	33	13	39	143							10		15		31		68	23	9	186		80		25	28		
1272	1		100	96	105	9	150	162	8							46		39		36		20	82	24	29		56		59	17	19	1939 3374
2272	1		23	63	90	38	19	42	149							14		19		37		69	18	13	150		90		22	26		
1273	1		98	95	103	8	150	162	8							47		40		41		22	85	23	30		57		59	18	21	65.5.9.4.
2273	1		19	60	97	38	21	44	152							12		22		35		69	20	11	156		93		24	23		
1274	1		90	93	104	12	150	160	7							48		39		36		17	85	20	31		50		57	16	17	1846.10.23.11
2274	1		24	62	94	37	20	38	152							11		19		35		67	18	11	158		74		22	25		
1275	1		85	102	110	8	148	158	7							48		38		35		18	67	21	29		51		55	21	23	1934 1002
2275	1		24	61	90	40	22	37	149							16		21		32		62	21	11	160		78		25	22		
1276	1		85	100	109	9	146	156	7							45		36		36		17	76	24	31		54		56	16	22	M644
2276	1		16	62	87	36	22	37	139							11		19		27		73	22	15	174		79		19	31		
1277	1		75	90	97	8	140	151	8							46		36		37		18	78	24	28		56		58	15	23	FC 70
2277	1		19	59	86	35	20	35	140							9		17		26		63	24	11	164		94		23	25		
1278	1		60	94	100	6	145	156	8							43		36		39		20	85	24	30		56		59	18	21	47.3.1.5
2278	1		19	61	90	33	16	37	153							11		13		32		61	12	8	164		60		24	22		
1279	1		56	96	105	9	133	147	11							44		33		32		18	72	22	29		51		55	16	18	1934.1003
2279	1		17	60	88	32	18	32	142							10		15		24		62	15	12	166		83		22	21		
1280	1		55	90	96	7	142	151	6							42		33		35		14	72	21	31		47		49	19	22	1934 1004
2280	1		17	60	88	34	19	35	151							10		15		30		60	14	6	170		79		21	21		
1281	1		53	95	100	5	140	149	6							44		31		36		17	76	23	32		53		56	18	20	1939.997
2281	1		19	65	96	38	23	36	140							10		18		35		62	17	12	143		79		23	25		
1282	1		52	91	99	9	139	148	6							44		37		35		16	73	23	30		53		57	17	21	1948 3221
2282	1		19	64	89	32	18	35	151							8		15		25		60	18	11	185		61		17	21		
1283	1		48	89	95	7	129	137	6							41		34		31		15	70		27		47		51	18	19	1939980
2283	1		20	66	90	33	18	33	152							9		16		34		58	12	9	132		71		21	22		
1284	1		52	86	93	8	129	137	6							41		31		33		15	67	20	22		48		49	18	20	1939979
2284	1		17	65	89	33	18	33	155							8		15		26		58	15	15	162		64		22	24		

CARD2.

CARD1.

CARD NO. / TAXON NO. / SPECIMEN NO. / SEX / JUVENILE/ADULT	RDA	CC-TP ♂ MAX W.	♀ X RAY W.	% DIST. W.	IT-IT/TP-TP MAX L.	FO-FO/TP-TP X RAY L.	IT-IT / BS % DIST. L.	IT-IT	FO-FO	CC-CC	PA-PA	TP-TP	FM-FM	BS-OP	SP-SP	SM-SM	SB-BS	PS-SB	CC-PA	
1285 1	50	89	96	8	135	145	7	39	36	39	20	70	21	30	52	50	16	19		1939 1004
2285 1	11	63	90	32	16	30	150	8	15	29	63	18	8	166	70	20	19			
1286 1	42	94	100	6	128	138	8	43	37	34	16	71		28	52	57		21		U2
2286 1	19	62	90	33	19		141	11	19	35	58	15	12	172	63	22	23			
1287 1	41	94	100	6	132	141	7	40	36	37	15	65		27	53	56		20		48.4.39.
2287 1	13	59	78	28	14		155+	9	15	28	66	14	8	170	79	20	21			
1288 1	40	86	92	7	136	145	7	41	37	35	13	65		28	50	54		19		1939.62
2288 1	14	58	77	25	17	32	144	8	14	28	65	16	9	178	87	19	24			
1289 1	36	92	99	8	128	139	9	38	34	36	18	66	23	28	51	55	14	20		M152
2289 1	14	60	74	28	15	34	142	6	13	25	57	18	11	168	76	16	24			
1290 1	32	90	95	6	130	139	7	40	34	31	17	65		28	48	53		18		48.438
2290 1	16	66	80	31	17		154	7	16	25	59	18	9	135	74	16	18			
1291 1	30	87	93	7	126	133	6	42	35	35	14	63	20	26	48	53	16	19		1939.1000
2291 1	14	62	78	28	16	34	150	10	16	31	60	14	10	160	80	19	20			
1292 1	25	92	98	7	124	133	7	41	33	27	15	62	20	24	43	46	15	17		M 888
2292 1	15	61	87	27	15	33	141	10	15	38	56	13	12	168	64	14	21			
1293 1	22	91	97	7	126	133	6	40	30	30	12	59	20	21	46	49	14	16		2H
2293 1	16	58	88	26	14	30	137	8	12	27	58	10	10	137	70	16	24			
1294 1	15	86	97	13	121	135	12	40	33	30	7	62	25	28	45	48	14	17		M 465
2294 1	11	55	90	30	17	32	148	11	16	28	61	13	11	144	60	21	25			
1295 1	20	92	100	9	124	140	13	44	36	35	16	63	21	29	51	55	14	20		M781
2295 1	12	51	76	28	14	32	143	10	18	28	64	13	10	160	48	20	25			
1296 1	10	87	94	8	123	130	6	37	31	27	13	51	19	24	44	46		18		CAM II 34
2296 1	13	62	86	26	15	33	143	8	16	29	53	14	7	163	54	18	22			
1297 1	7	90	93	3	126	130	3	41	33	34	13	53	20	26	53	53	14	20		M 475
2297 1	13	55	88	25	13	30	143	8	16	24	56	15	8	174	46	17	21			
1298 1	2	82	88	7	109	119	9	35	28	22	12	42	16	24	43	45		14		M 202
2298 1	10	68	80	21	10	25	150	8	13	31	55	12	7	173	80	17	18			
GORILLA ADULT 140122	22	138	145	5	210	228	9	53	42	44	24	119	29	30	61	72	25	29		1951.9.27.13
240122	39	70	96	56	26	62	154	21	25	28	64	30	28	18	92	19	35			
140222	22	144	154	7	225	245	9	60	51	44	26	124	26	30	65	82	29	28		1939 956
240222	38	72	96	56	28	62	155	21	27	36	65	28	28	16	70	22	35			
140322	22	135	146	8	230	247	7	56	52	45	27	126	30	28	69	79	30	30		1939 936
240322	39	74	98	60	27	62	153	22	31	39	68	30	26	12	80	17	37			
140422	22	131	145	11	227	240	6	51	51	45	33	122	26	29	64	77	29	30		1939 933
240422	36	77	95	58	33	62	160	21	28	37	70	33	19	13	85	18	37			
140512	22	160	175	9	266	284	7	57	52	45	29	137	28	35	64	81	30	29		1939 932
240512	44	74	94	62	32	69	156	25	35	44	74	35	31	15	100	20	44			
140622	22	141	150	6	225	244	8	54	48	42	29	126	27	32	61	76	25	20		1939 922
240622	41	75	98	52	25	52	160	20	27	34	61	27	26	13	72	23	26			
140722	22	147	157	7	235	265	13	57	50	50	29	129	29	32	69	76	31	32		1939 925
240722	37	70	94	55	25	59	150	21	29	34	68	30	26	16	89	22	34			
140822	22	137	148	8	220	242	10	61	51	47	29	121	25	29	60	72	29	37		1939 927
240822	36	69	100	56	32	60	157	19	31	40	62	29	30	14	88	23	28			
140922	22	145	156	8	242	265	10	55	48	45	27	128	28	32	63	76	32	29		1948.12.20.2
240922	42	72	97	61	35	66	153	23	30	33	65	36	29	17	86	20	35			
141012	22	164	177	8	260	290	12	62	57	51	31	128	29	30	67	80	32	31		1939. 950
241012	42	71	90	57	28	65	159	23	34	36	72	35	29	19	94	26	27			
141122	22	147	157	7	235	258	10	65	53	40	29	131	28	30	65	78	33	27		1939. 541
241122	43	79	90	54	29	64	152	25	36	38	75	28	31-	15	89	18	37			
141212	22	175	194	11	306	334	9	60	55	55	36	159	31	34	64	77	34	28		1939. 954
241212	45	71	97	72	38	84	165	33	38	40	75	40	29-	17	146	21	36			
141312	22	173	189	9	278	310	12	61	52	46	33	145	24	34	65	82	32	35		1439 928
241312	46	77	94	65	32	71	161	27	35	42	71	40	24-	16	95	24	34			
141412	22	163	174	7	274	295	8	60	52	44	33	126	26	29	65	88	34	32		1939 921
241412	40	81	92	66	36	74	158	31	36	41	75	32	33-	17	90	21	34			
141512	22	170	187	10	288	310	8	67	54	42	29	138	29	32	62	80	36	31		1948 4.1.1
241512	46	77	93	65	34	77	163	26	32	38	70	35	28-	14	98	22	33			
141612	22	161	175	9	265	294	11	60	47	49	30	131	25	33	63	75	35	32		1939. 940
241612	41	76	99	75	38	85	165	23	30	37	70	35	26	15	97	23	35			
141722	22	147	158	8	229	252	10	60	52	51	34	137	28	30	67	80	32	34		1939. 950
241722	34	75	102	75	37	74	152	17	33	42	73	29	31	17	80	25	39			
141812	22	149	161	8	274	303	11	54	48	41	29	131	28	30	63	75	31	30		A 26
241812	43	77	94	63	36	69	157	22	32	37	64	37	30	14	100	24	33			
141922	22	152	165	9	240	265	10	56	55	49	30	133	29	33	63	77	33	29		23.11.29.8
241922	42	72	94	65	30	74	156	26	32	37	70	30	32	15	90	18	41			

CARD2.

CARD1.

CARD NO. / TAXON NO. / SPECIMEN No. / SEX / JUVENILE / ADULT	CC-TP RDA	MAX W. α	X RAY W. β	% DIST. W. IT-IT/TP-TP	MAX L. FO-FO/TP-TP	X RAY L. IT-IT / BS γ	% DIST. L.	IT-IT MO-MO	FO-FO OC-OC	CC-CC SOF-SOF	PA-PA PT-PT	TP-TP IT-HA	FM-FM NA-FC	BS-OP FC-CL	SP-SP CR-CR	SM-SM FC-PS	SB-BS PS-SB	CC-PA	
142022	22	140	149	6	226	239	6	58	50	45	29	119	27	28	62	72	30	26	1939 913
242022	35	74	93	55	29	63	151	22	33	41	65	35	26	12	95	20	32		
142122	22	151	162	7	230	255	11	62	56	50	34	132	32	33	71	81	32	28	1939 948
242122	41	71	100	60	30	67	158	25	34	40	72	32	22	14	78	22	37		
142212	22	170	182	7	296	335	13	63	53	55	34	150	30	36	72	89	35	33	78.12.14.1.
242212	44	73	88	67	33	80	166	28	34	40	73	40	34	17	90	18	38		
142322	22	143	159	11	230	254	10	57	51	46	26	129	30	34	62	78	29	30	1939.929
242322	41	72	98	61	31	61	156	23	30	37	67	27	28	14	90	19	34		
142412	22	168	179	6	295	334	13	60	55	57	33	136	28	30	72	89	31	27	1939 934
242412	37	60	97	59	28	63	152	25	31	34	73	45	28	16	96	24	34		
142512	22	177	188	6	310	340	10	67	53	50	33	144	31	32	70	82	35	29	M505
242512	44	68	96	69	35	78	155	33	27	41	74	40	23	15	86	20	35		
142612	22	142	162	14	230	260	13	58	57	47	31	136	33	37	72	89	35	35	M342
242612	43	70	95	75	34	79	149	25	30	36	78	30	23	14	100	20	40		
142712	22	156	177	13	257	275	7	59	51	51	32	135	32	33	68	84	26	27	M241
242712	39	66	93	57	31	64	150	26	32	35	71	38	36	15	80	27	40		
142812	22	156	176	13	271	300	11	64	47	45	29	121	31	34	69	87	35	30	M462
242812	35	69	93	60	29	70	159	30	28	35	74	33	31	15	110	24	41		
142912	22	148	164	11	234	264	13	63	53	57	33	135	30	37	70	82	36	27	M89
242912	37	60	96	69	35	78	150	30	31	40	71	40	36	14	90	22	33		
143022	22	141	155	10	230	260	13	53	47	45	28	116	29	30	65	74	33	30	M86
243022	35	67	92	60	29	70	159	24	28	36	72	34	31	18	90	26	31		
GORILLA 2431 1	210156	176	13	271	300	11	64	47	45	29	121	31	34	69	87	35	30	M241	
JUVENILE 2431 1	35	69	93	60	29	70	159	30	28	35	74	33	31	15	110	24	41		
1432 1	217161	175	9	265	294	11	60	47	49	30	131	25	33	63	75	35	32	1939.940	
2432 1	41	76	99	75	38	85	165	23	30	37	70	35	26	15	97	23	35		
1433 1	200129	136	5	215	234	9	51	42	44	32	110	28	29	62	70	29	30	28.4.49	
2433 1	34	70	87	55	26	62	155	19	26	35	67	26	26	16	88	21	35		
1434 1	174144	153	6	225	240	7	56	49	49	27	123	31	30	65	78	22	27	10.11.27.1	
2434 1	37	67	97	58	30	57	157	25	33	39	80	30	31	16	88	24	42		
1435 1	172141	152	8	225	240	7	59	47	47	28	120	28	31	61	70	30	27	M857	
2435 1	35	66	94	57	31	64	157	21	27	37	71	27	32	16	84	23	39		
1436 1	170134	143	7	225	244	8	55	49	48	30	117	25	35	62	76	30	30	1939455	
2436 1	35	75	98	62	33	61	157	16	27	38	68	25	28	17	80	25	31		
1437 1	170130	139	7	211	240	14	53	42	40	30	114	27	30	60	72	28	28	FC114	
2437 1	34	63	91	49	26	55	151	19	24	33	70	23	23	15	106	24	32		
1438 1	150133	142	7	219	233	6	52	45	48	27	117	26	34	62	75	34	30	1857.11.22	
2438 1	32	68	102	59	29	58	157	20	28	37	75	28	22	14	90	23	32		
1439 1	140131	141	8	220	235	7	57	45	40	24	104	24	33	54	69	34	26	522.26.2	
2439 1	36	71	102	55	32	61	153	16	28	38	68	28	25	18	78	23	23		
1440 1	132137	147	7	235	268	14	54	50	50	27	126	26	39	60	70	34	30	M689	
2440 1	35	66	95	58	29	54	162	21	24	33	67	25	21	14	85	21	37		
1441 1	130133	142	7	225	262	16	53	49	47	30	106	29	32	61	71	27	22	M674	
2441 1	28	66	94	49	20	52	157	18	23	32	68	30	12	15	110	22	40		
1442 1	130128	140	9	200	223	12	52	45	47	23	115	29	37	60	71	22	28	MER II.1.	
2442 1	35	56	96	49	20	53	145	17	22	33	64	23	22	16	94	26	38		
1443 1	127134	143	7	220	245	11	58	52	44	31	116	30	39	68	76	31	27	M22	
2443 1	35	72	95	53	21	59	162	16	22	34	78	25	17	15	95	23	38		
1444 1	125130	140	8	218	245	12	52	45	45	25	113	29	31	62	71	28	29	M180	
2444 1	35	61	94	52	22	57	158	18	24	31	65	18	24	18	85	22	38		
1445 1	124130	139	7	207	227	10	52	48	47	26	105	27	35	60	76	22	27	M485	
2445 1	33	63	90	51	28	54	156	18	24	31	65	18	21	15	99	23	34		
1446 1	123129	138	7	200	222	11	53	47	45	26	114	27	33	62	73	25	25	M667	
2446 1	33	62	97	53	28	56	158	22	27	33	65	20	27	16	101	24	38		
1447 1	123126	136	8	211	238	13	52	45	47	30	103	31	35	65	78	28	30	M387	
2447 1	32	65	85	51	30	64	155	25	28	33	65	20	20	19	88	25	34		
1448 1	122131	141	8	215	228	6	54	48	45	26	115	32	33	63	73	28	28	M841	
2448 1	32	66	95	52	26	54	156	19	26	31	72	28	27	14	97	20	35		
1449 1	122130	143	10	212	235	11	51	47	50	28	124	32	38	69	78	28	28	M875	
2449 1	35	60	95	51	29	56	157	21	24	31	67	27	22	19	105	25	37		
1450 1	120132	147	11	220	237	8	54	49	48	26	123	25	27	64	72	28	25	29.11.3.	
2450 1	29	67	100	58	29	59	162	20	28	32	62	30	23	18	105	23	37		
1451 1	120130	142	9	215	235	9	48	48	46	27	128	29	36	66	77	27	28	M691	
2451 1	30	68	90	56	22	57	154	21	26	31	65	27	28	16	105	21	38		
1452 1	112127	136	7	204	220	8	52	43	43	22	107	27	29	60	69	22	27	M160	
2452 1	30	65	96	51	26	51	155	17	25	34	64	25	23	16	83	22	44		

CARD2.

CARD1.

CARD NO.	TAXON NO.	SPECIMEN No.	SEX	JUVENILE/ADULT	CC-TP RDA	MAX W. α	X RAY W. β	% DIST. W. IT-IT/TP-TP	MAX L. FO-FO/TP-TP	X RAY L. IT-IT/BS γ	% DIST. L.	IT-IT MO-MO	FO-FO OC-OC	CC-CC SOF-SOF	PA-PA PT-PT	TP-TP IT-HA	FM-FM NA-FC	BS-OP FC-CL	SP-SP CR-CR	SM-SM FC-PS	SB-BS PS-SB	PA CC-PA	
1453	1				110	113	118	4	187	205	10	52	46	40	25	102	28	33	67	76	24	23	FC 114
2453	1				28	65	95	50	26	50	160	13	21	30	65	30	17	18	100	24	37		
1454	1				105	128	137	7	225	234	4	58	48	55	29	110	29	33	63	79	31	29	M 847
2454	1				30	59	90	50	24	55	156	18	23	32	71	35	26	16	86	22	29		
1455	1				104	127	135	6	205	230	12	49	43	44	21	113	25	31	65	75	20	29	936.32.51
2455	1				29	65	94	51	27	45	152	12	22	30	60	26	25	19	94	21	38		
1456	1				104	114	121	6	190	201	6	52	45	45	24	99	28	26	60	71	19	23	61.7.29.27
2456	1				34	70	98	50	25	40	148	16	25	35	60	28	21	17	90	21	35		
1457	1				103	128	134	5	195	213	9	50	48	46	28	107	30	30	70	76	25	24	29.11.2
2457	1				37	68	90	51	26	52	151	16	24	32	61	25	21	19	98	22	34		
1458	1				99	115	121	5	181	193	7	52	44	40	20	89	25	33	59	67	20	24	1939.937
2458	1				24	66	95	43	26	45	157	13	22	33	68	21	16	15	94	21	30		
1459	1				98	121	126	4	185	195	5	49	43	42	22	99	26	31	67	69	22	22	20.4.13.5
2459	1				29	66	93	46	25	44	159	13	22	30	70	27	20	16	97	23	31		
1460	1				95	120	126	5	190	210	11	50	45	46	26	104	29	34	67	75	21	27	M 855
2460	1				30	63	90	44	23	41	152	14	22	30	64	25	19	16	86	20	34		
1461	1				90	117	123	5	185	201	9	50	45	45	26	101	31	36	62	79	24	23	M 463
2461	1				27	63	82	42	22	42	145	17	23	29	58	22	17	20	100	25	34		
1462	1				85	116	121	4	184	197	7	49	43	41	22	98	25	30	58	69	21	25	1939.959
2462	1				27	68	96	45	27	44	158	14	23	35	64	23	19	16	98	19	33		
1463	1				78	117	122	4	185	200	8	54	47	43	25	98	28	33	62	70	28	24	2341.29.9
2463	1				27	71	90	46	25	45	160	14	26	32	66	19	17	19	95	23	30		
1464	1				75	108	111	3	169	180	7	45	39	47	21	89	30	25	64	70	23	24	36.7.73
2464	1				21	61	93	39	19	42	155	11	18	30	62	19	13	19	90	26	34		
1465	1				70	·	·	·	161	172	7	45	43	44	24	·		26	60	74	17	25	1011 J
2465	1				21	65	89	39	21	39	150					18	13	16		21	35		
1466	1				65	113	118	4	181	204	13	52	42	45	23	88	29	33	64	72	24	25	M 1880
2466	1				20	59	82	39	19	42	150	13	20	32	68	22	17	17	94	23	34		
1467	1				62	109	118	8	173	187	8	46	44	43	23	95	25	30	60	70	20	22	M 000
2467	1				26	60	95	40	24	40	150	12	17	26	63	24	20	17	80	23	31		
1468	1				61	106	113	7	175	192	10	49	43	41	22	97	27	31	61	69	27	22	M 333
2468	1				29	58	90	38	21	46	161	13	20	34	69	17	17	19	94	23	34		
1469	1				60	112	114	2	173	188	9	50	48	45	24	89	27	33	63	72	22	22	M 487
2469	1				20	54	96	37	22	38	150	11	17	28	69	21	12	18	75	24	31		
1470	1				60	115	120	4	180	196	9	48	41	42	23	97	28	36	58	69	19	24	M 471
2470	1				27	59	92	41	24	41	144	14	20	28	63	22	16	20	98	23	34		
1471	1				55	115	122	6	179	195	9	50	45	44	26	96	31	36	67	71	17	23	M 99
2471	1				23	57	93	41	20	42	141	12	20	28	63	22	14	18	103	24	29		
1472	1				54	103	113	10	164	174	6	47	40	39	20	84	25	27	54	63	23	20	M 409
2472	1				21	55	86	32	13	33	141	10	22	30	69	17	18	17	90	21	30		
1473	1				53	113	120	6	171	186	9	51	45	47	21	95	32	32	63	72	25	24	M 532
2473	1				22	49	85	36	20	39	141	8	21	33	65	15	17	20	68	25	32		
1474	1				52	98	106	8	152	165	9	46	41	40	21	81	22	27	57	63	21	20	1011 K
2474	1				20	65	86	36	17	41	151	11	20	31	61	17	15	19	100	23	30		
1475	1				52	95	103	8	160	170	6	45	41	39	22	83	23	31	55	64	16	22	1939 960
2475	1				22	69	84	35	22	35	153	10	20	32	61	20	15	18	92	22	28		
1476	1				51	102	112	10	161	176	9	46	43	43	21	87	29	30	63	70	21	23	M 117
2476	1				23	53	87	35	21	37	148	11	19	31	60	20	11	15	90	20	32		
1477	1				50	102	108	6	158	169	7	46	39	42	23	82	29	33	56	65	20	21	61.5.14.2
2477	1				21	66	81	41	24	38	148	9	20	33	58	19	15	18	102	26	33		
1478	1				35	98	103	5	152	161	6	43	40	39	20	80	26	34	57	66	16	19	1939.962
2478	1				20	59	84	35	19	33	146	10	18	30	60	15	14	19	85	20	29		
1479	1				34	85	88	4	110	112	2	47	37	37	16	69	22		52	59	21	21	1939.902
2479	1				16	61	70	32	18	37	164	9	16	27	60	14	13	17	76	23	34		
1480	1				28	101	109	8	145	154	6	45	37	38	22	61	26	31	54	62	16	20	M 756
2480	1				15	58	86	31	18	38	141	8	15	24	61	14	12	15	82	19	29		
1481	1				20	96	105	9	140	153	9	45	37	33	16	66	27	34	48	57	18	18	M 887
2481	1				16	59	84	30	18	31	149	7	17	24	57	15	9	20	75	23	24		
1482	1				18	90	93	3	139	149	7	43	36	37	17	69	22	29	49	56	19	19	CAM I·43.
2482	1				18	57	83	29	18	33	158	8	15	28	61	12	11	15	70	20	20		
1483	1				18	100	108	8	152	163	7	44	39	37	17	67	22	35	50	59	16	22	FC 129
2483	1				15	58	80	31	15	38	150	8	18	25	60	16	11	16	66	23	25		
1484	1				15	94	98	4	141	151	7	42	37	35	15	64	25	29	50	60	18	20	1011 Q
2484	1				15	61	75	31	16	36	155	9	18	28	55	12	8	18	90	25	26		
1485	1				12	89	96	8	131	140	7	39	35	32	17	60	22	30	51	58	15	18	1939.983
2485	1				14	65	73	26	141	29	149	7	15	24	55	12	8	13	69	17	23		

CARD 2.

CARD 1.

CARD NO.	TAXON NO.	SPECIMEN No.	SEX	JUVENILE/ADULT	RDA	CC-TP	MAX W.	α	X RAY W.	β	% DIST. W.	IT-IT/TP-TP	MAX L.	FO-PO/TP-TP	X RAY L.	IT-IT/BS	% DIST. L.	χ	IT-IT	MO-MO	FO-FO	OC-OC	CC-CC	SOF-SOF	PA-PA	PT-PT	TP-TP	IT-HA	FM-FM	NA-FC	BS-OP	FC-CL	SP-SP	CR-CR	SM-SM	FC-PS	SB-BS	PS-SB	CC-PA	
		1456	1		7		94		102		9		142		153		8		42	33	36	20	65		30		55	59	18	20	M476
		2486	1		16		65		81		32		18		37		158		12	16	25	57	12	10	19		65	24	25		
		1487	1		6		90		97		8		118		124		5		40	29	22	11	49	25	23		38	43	14	14	22.12.198
		2487	1		13		62		75		20		10		33		148		8	14	24	50	10	13	12		78	15	22		
		1488	1		5		88		92		5		130		141		8		46	34	35	15	66	22	31		44	53	12	21	1948.437
		2488	1		15		69		76		31		18		32		146		11	20	31	60	14	9	14		57	14	21		
		1489	1		2		78		83		6		118		123		4		39	33	32	14	58	19	23		45	50	12	18	1846.12.12
		2489	1		13		58		77		26		15		30		159		8	15	26	55	8	9	14		72	16	25		
DONGO:		160112			22		166		178		7		235		259		10		55	48	52	32	132	25	31		66	77	35	29	1939/1018
ADULT		260112			40		70		98		61		28		68		150		16	24	41	74	25	23	111		110	111	40		
		160222			22		136		143		5		191		209		9		50	42	48	21	106	24	29		68	76	29	29	026
		260222			34		70		99		55		27		59		150		11	20	37	75	20	25	94		80	94	38		
		160322			22		126		133		6		192		207		8		55	43	48	29	105	25	31		72	77	27	23	029
		260322			32		67		104		44		27		47		150		12	21	40	60	23	13	150		106	150	38		
		160412			22		131		138		5		196		209		7		47	43	49	30	106	25	28		75	80	31	28	034
		260412			32		70		97		53		24		62		148		11	22	41	75	24	19	156		89	156	38		
		160522			22		131		136		4		194		208		7		51	45	50	28	101	31	32		71	75	26	27	012
		260522			30		69		97		52		23		57		151		11	21	32	71	23	24	122		84	122	39		
		160612			22		163		173		6		225		248		10		49	48	51	32	122	21	26		69	76	33	29	45.10.21
		260612			33		69		99		65		28		73		150		16	26	46	63	30	22	134		108	134	48		
		160712			22		173		185		7		231		259		12		60	46	52	30	137	24	34		66	78	33	31	92.11.55
		260712			41		65		98		65		30		75		158		20	25	46	66	31	30	130		88	130	49		
		160812			22		162		172		6		210		229		9		51	54	52	31	121	24	31		67	78	37	29	1080
		260812			33		69		102		64		29		70		155		17	23	35	70	29	25	115		80	115	45		
		160922			22		170		180		6		214		239		12		48	46	52	32	123	25	30		72	76	30	32	1011
		260922			35		72		104		64		32		64		152		12	19	38	71	30	27	130		80	130	41		
		161012			22		165		176		7		216		244		13		55	50	54	37	127	28	32		75	86	29	25	1085
		261012			35		65		108		64		32		64		140		11	23	36	68	27	24	120		80	120	39		
		161112			22		160		168		5		207		230		11		50	44	52	32	120	24	26		64	69	29	28	3B
		261112			39		70		100		59		29		64		151		13	25	43	60	25	24	120		100	120	41		
		161212			22		171		185		8		230		266		16		54	49	60	30	131	25	30		70	76	32	33	1939 1008
		261212			32		75		109		70		38		71		150		18	24	44	65	25	26	100		83	100	42		
		161322			22		145		152		5		212		224		6		58	45	48	27	117	25	35		57	65	29	28	1939 1007
		261322			38		68		105		58		27		59		145		12	25	38	79	29	22	120		102	120	40		
		161412			22		151		159		5		200		218		9		55	48	47	31	119	23	32		61	70	27	24	3EE
		261412			30		71		108		60		30		61		150		17	23	43	78	24	25	124		80	124	36		
		161522			22		130		136		5		190		206		8		54	45	48	29	113		35		73	78	27	25	1099.3W.
		261522			32		68		102		50		25		56		145		11	22	37	71	25	22	113		74	113	40		
		161612			22		136		145		7		212		230		9		48	47	53	27	113	26	26		72	81	28	30	1939.10.19
		261612			32		69		100		56		27		61		150		7	20	42	72	25	19	130		90	130	38		
		161722			22		128		135		6		196		211		8		48	45	48	28	110	22	31		64	74	29	28	1948.11.23.1
		261722			30		70		99		57		27		60		148		10	22	40	68	22	23	115		80	115	35		
		161822			22		131		137		5		179		197		10		48	41	46	27	103	23	26		77	83	27	25	1948.7.6.1
		261822			41		67		98		46		21		51		146		10	19	34	61	23	20	145		80	145	32		
		161912			22		174		183		5		242		254		5		56	45	48	33	132	21	32		71	79	34	31	030
		261912			34		65		95		62		27		69		152		14	25	41	67	30	25	160		108	160	41		
		162012			22		164		173		6		224		244		9		57	49	57	30	129	23	33		65	74	30	32	1948.7.6.3
		262012			40		68		98		63		27		66		148		17	24	43	71	27	23	115		103	115	43		
		162112			22		162		173		7		217		251		16		46	40	45	26	125	24	24		66	78	35	28	3m²
		262112			37		69		98		61		28		70		153		17	26	36	62	27	23	135		80	135	50		
		162212			22		137		148		8		204		219		7		63	45	43	30	120	23	35		67	78	24	23	72.167.
		262212			32		69		100		55		26		56		140		10	23	41	75	27	23	128		101	128	35		
		162312			22		164		173		6		226		245		8		50	50	55	35	122	25	35		72	76	28	27	1948 10 25.1
		262312			32		70		106		60		30		59		152		15	26	42	69	34	25	130		85	130	41		
		162422			22		135		142		5		198		216		9		51	42	48	29	113	26	34		75	86	26	27	1948 10 30.1
		262422			40		67		96		55		24		61		150		11	19	32	61	20	26	130		76	130	35		
		162512			22		161		174		8		216		241		12		46	40	51	24	137	23	31		64	69	35	35	73.15.70
		262512			27		70		93		60		27		69		154		14	12	40	57	27	30	146		93	146	36		
		162622			22														50	39	43	27	107	24	33		61	68	21	26	A63.50
		262622			31		63		105		44		24		45																							
		162722			22														54	42	47	23	101	24	30		69	75	30	28	A63.61
		262722			33		60		102		54		28		58																							
		162822			22														46	41	41	31	128	23	32		55	65	26	24	A63.54
		262822			40		68		102		52		23		53																							
		162912			22														53	48	57	27	103	29	29		70	82	38	32	A63.56
		262912			35		62		105		69		37		66																							

CARD 2.

CARD 1.

DONGO
JUVENILE

CARD NO. / TAXON NO. / SPECIMEN NO. / SEX / JUVENILE/ADULT	CC-TP RDA	MAX W.	X RAY W,	% DIST. W.	IT-IT'/TP-TP MAX L.	FO-FO'/TP-TP X RAY L.	IT-IT'/BS % DIST. L.	MO-MO IT-IT	OC-OC FO-FO	SOF-SOF CC-CC	PT-PT PA-PA	IT-HA TP-TP	NA-FC FM-FM	FC-CL BS-OP	CR-CR SP-SP	FC-PS SM-SM	PS-SB SB-BS	CC-PA	
163022	22							55	43	48	24	102	25	31	70	76	31	29	A63.59
263022	34	61	102	54	28	58													
163121	195	135	142	5	198	216	9	61	42	48	24	113	26	34	75	86	26	27	48.10.31
263121	40	67	96	55	24	61	150	11	19	32	61	20	26	130	76	130	35		
163221	185	129	135	5	196	211	8	48	45	48	27	103	22	31	64	74	29	28	48.11.23.1
263221	30	70	99	57	27	60	148	10	22	40	68	22	23	115	80	115	35		
163311	190	136	145	7	212	230	8	48	47	53	28	110	26	26	72	81	28	30	1939.1019
263311	32	69	100	56	27	61	150	7	20	42	72	25	19	130	90	130	38		
1634 1	175	121	127	5	188	204	9	51	43	49	25	111			60	70	23	26	043
2634 1	32	65	104	54	29	52	145	7	15	36	75	16	20	110	65	110	33		
1635 1	170	123	130	6	184	201	9	54	40	49	27	106			65	71	26	24	046
2635 1		68	104	54	29			9	17	34	62	16	19	130	80	130	34		
1636 1	170	127	135	6	185	203	10	55	50			109			70	78			1976.14.41
2636 1	28	69	100	49	25			8		36	76	22	19	100	70	100			
1637 1	162	117	133	14	185	199	8	52	41	50	25	114			67	73	25	26	032
2637 1	31	69	104	49	25	52	140	8	17	32	72	17	21	125	85	125	30		
1638 1	160	112	120	7	173	186	8	48	38	44	20	104			64	65	25	30	045
2638 1	30	69	92	50	24	56	150	7	15	35	68	20	19	110	60	110	29		
1639 1	150	111	118	6	167	185	11	48	38	41	22	97	22	30	55	68	20	21	110
2639 1	29	69	104	49	25	49	160	9	18	31	71	22	19	137	74	137	32		
1640 1	147	109	119	9	161	190	18	47	40	40	20	100	26	30	58	67	23	22	CA30 CGC 44
2640 1	24	60	103	46	24	50	152	8	17	36	76	19	17	135	72	135	37		
1641 1	150	109	115	6	174	179	3	49	38	46	25	95	26	34	56	65	25	28	ADC 14. CH 22
2641 1	30	70	98	46	21	52	145	7	18	37	71	18	17	125	60	125	35		
1642 1	120	102	112	10	160	176	10	47	38	41	22	96	24	33	61	71	20	24	CH 28
2642 1	29	68	90	37	16	43	143	5	18	36	70	13	17	130	80	130	23		
1643 1	110	98	101	3	146	157	8	48	36	38	19	83	25	31	55	61		20	1976.14.13
2643 1	25	63	101	37	19	37	147	7	18	37	64	15	16	125	60	125	25		
1644 1	120	92	103	12	149	154	3	48	35	44	21	90		32	55	62	19	23	1844.3307
2644 1	23	60	100	37	19	37	150	7	13	28	72	19	16	110			25		
1645 1	112	107	114	7	170	183	8	51	41	44	24	97	25	37	62	70	20	25	443.2.08
2645 1	24	65	100	40	22	40	150	6	15	37	70	17	19	115	90	115	31		
1646 1	102	113	122	8	181	197	9	52	39	41	25	105	25	37	63	72	24	25	1976 14 10
2646 1	31	70	94	42	21	44	144	5	18	36	62	18	19	120	70	120	30		
1647 1	105	102	116	14	165	179	8	53	39	46	23	98	24	35	60	67	21	26	1852 52 12.
2647 1	27	63	98	48	24	50	145	6	19	36	74	19	17	120	85	120	29		
1648 1	110	110	117	6	174	188	8	48	39	45	23	100	22	38	63	71	22	25	1082
2648 1	27	62	92	45	23	50	149	7	18	36	74	19	22	115	80	115	30		
1649 1	113	96	103	7	161	176	9	47	34	39	19	85	21	34	51	58	18	21	CH 25.
2649 1	24	60	102	43	22	43	149	8	16	26	68	20	17	109	98	109	31		
1650 1	110	107	113	6	164	176	7	46	38	45	21	93	23	30	60	65	21	27	35
2650 1	23	60	100	43	22	47	142	7	24	29	65	17	20	105	60	105	32		
1651 1	100	107	114	7	164	179	9	50	39	45	21	97	26	36	61	71	22	25	A65.13
2651 1	24	65	98	43	25	48	152	8	18	32	64	18	18	152	90	152	35		
1652 1	102	102	109	7	160	175	9	48	36	41	21	91	23	32	58	66	19	24	A65.12
2652 1	25	65	99	43	24	45	154	7	18	33	65	21	17	140	80	140	33		
1653 1	104	101	114	13	159	173	9	50	35	41	20	93	25	31	55	64	18	25	1948.8.31
2653 1	27	70	100	46	24	48	153	7	17	34	67	19	20	125	85	125	31		
1654 1	95	108	112	4	161	176	9	48	39	46	22	85		37	60	65	20	22	1859.2.10.2
2654 1	19	60	100	41	22	46	160	10	18	36	70	15	15	160	95	160	29		
1655 1	93	97	105	8	148	163	10	43	33	42	18	84	26	32	57	65	17	23	A651
2655 1	20	59	90	35	19	39	150	7	15	31	60	15	15	140	85	140	27		
1656 1	88	93	101	9	159	173	9	52	35	44	21	87	26	34	55	62	20	21	$3i^2$
2656 1	21	60	100	45	22	48	155	7	21	33	72	17	15	125	65	125	25		
1657 1	90	100	109	9	152	163	7	49	38	45	25	90	22	30	61	64	23	23	3u
2657 1	26	69	105	43	23	45	140	7	18	36	68	22	15	120	70	120	30		
1658 1	91	97	104	7	149	161	8	45	36	39	19	87		35	55	63	17	19	3t
2658 1	25	58	100	36	19	36	154	6	18	37	66	17	15	120	65	120	25		
1659 1	82	92	99	8	148	164	11	47	36	42	20	86	21	34	54	61	20	21	A65.11
2659 1	25	62	105	41	22	41	145	8	15	23	66	18	14	110	70	110	28		
1660 1	68	101	108	7	162	173	7	49	40	47	22	91	26	37	62	67	19	21	50.8.15.1
2660 1	23	65	100	46	22	50	155	7	19	36	67	19	17	100	85	100	30		
1661 1	65	92	99	8	147	160	9	45	34	48	19	83	26	34	59	64	18	24	A656(5)
2661 1	17	50	100	41	23	47	146	8	16	33	64	14	14	140	95	140	25		
1662 1	63	93	99	6	145	156	8	43	37	40	20	74	21		55	60	19	19	1976.14.12
2662 1	18	58	110	35	20	34	146	7	16	29	64	14	18	130	95	130	23		

CARD2.

CARD1.

CARD NO.	TAXON NO.	SPECIMEN NO.	SEX	JUVENILE/ADULT	CC-TP	RDA	MAX W. α	X RAY W. β	% DIST. W.	IT-IT/TP-TP	MAX L.	FO-FO/TP-TP	X RAY L.	IT-IT/BS γ	% DIST. L.	MO-MO	IT-IT	OC-OC	FO-FO	CC-CC	SOF-SOF	PT-PT	PA-PA	IT-HA	TP-TP	NA-FA	FM-FM	FC-CL	BS-OP	CR-CR	SP-SP	FC-PS	SM-SM	PS-SB	SB-BS	CC-PA	
1663	1				65	93	100		8	141	152		8	45	33	36	19	77					52	57			20	3X
2663	1				21	64	100		36	18			155	8	16	31	62	15	16	130			100	130	27				
1664	1				50	92	97		5	131	140		7	37	32	35	19	71	24	30			53	59	23		19	67.4.1.22.
2664	1				19	65	92		29	17	34		158	6	16	25	65	13	12	145			70	145	19			
1665	1				55	95	101		6	145	158		9	44	36	45	21	80	24				56	63	18		21	1976.1411.
2665	1				21	60	95		34	17	38		145	4	13	32	66	13	15	130			85	130	18			
1666	1				60	100	106		6	143	155		8	45	35	40	19	78	29				52	58	22		22	3W
2666	1				21	60	100		30	17	34		148	7	16	36	72	15	13	145			70	145	24			
1667	1				40	95	101		6	141	157		11	43	35	40	20	73		33			54	59	17		21	1.3.74
2667	1				16	60	98		31	18	36		150	6	16	32	63	12	13	110			70	110	22			
1668	1				43	91	97		7	137	155		13	43	34	39	19	70	23	26			49	57	19		19	67.4.1.21
2668	1				15	60	99		35	20	38		149	5	15	29	62	16	11	125			65	125	22			
1669	1				45	93	99		6	148	162		9	46	35	40	20	82	24	34			51	64	19		20	MDDX.I.
2669	1				21	65	100		35	19	40		145	8	15	31	66	16	16	140			96	140	27			
1670	1				30	83	90		8	122	133		9	40	30	30	15	60	20	25			43	50	15		18	CH.28.J.57
2670	1				15	63	100		29	16	34		150	5	15	34	66	14	9	130			86	130	20			
1671	1				25	84	91		8	120	132		10	43	32	34	14	70	20	29			48	54	14		19	CH.28.J.58
2671	1				17	59	89		29	14	33		147	5	12	27	63	13	10	130			70	130	19			
1672	1				12	89	97		9	120	131		9	40	33	34	18	73	22				47	55			18	CH.28.J.56
2672	1				19	62	98		29	17	36		134	5	13	29	64	11	10	132			66	132				
1673	1				10	90	94		4	118	122		3	43	30	31	14	63	22	23			47	54	14		18	67.4.12.3
2673	1				18	55	90		26	11	35		135	8	13	32	66	14	9	145			84	145	18			
FOSSIL HOMINIDS	1801	2												50	44	42	26	90									19	SES 25
	2801	2				19	72	104		48	37	40																	
	1802	2												49	44	50	25	89	22	27			63	68	20		20	SES 19
	2802	2				22	59	98		41	22	39	120																SES 71
	1803	2												45															
	2803	2								48	26		145																
	1804	2												54	43	51	22	100	20	27			68	78	12		20	SK47
	2804	2				25	45	102		45	23	37																	
	1805	2												62	46	44	21	98					60	63			20	SK847
	2805	2				23	50	110		49	31	41																	
	1806	2												61	41	50		118					66	67				TM1517
	2806	2					42	115		63	35	57																	
	1807	1												44	36	38	15	54							16		14	TAUNG
	2807	1				9	50	90		29	18	32																	
	1808	2												61	58	65	29	132	32	29			79	85	29		30	KNM ER 406
	2808	2				34	44	100		57	30	53																	
	1809	2												60	40	53	28	102	28	29			64	73	21		23	KNM ER 407
	2809	2				25	49	112		47	24	40																	
	1810	2												60	41	36	14	100									19	KNM ER 732
	2810	2				33	45	105		50			155																
	1811	2												65	51	55	20	103	26	29			66	72	22		24	KNM ER 1813
	2811	2				19	46	95		44	24	45	135																
	1812	2												61	49	48	23	103	25	29			67	72	16		20	OH.24
	2812	2				30	54	108		45	28	38	148																
	1813	2												70	45	60	25	131		30					25		25	KNM ER 1470
	2813	2				30	45	105		56	27	56	130																
	1814	2												60	44	48	20	118					72	78			20	KNM ER 1805
	2814	2				32	46	112		60	42	58	158																
	1815	2												69	54	57	31	115	26	31			78	84	24		25	KNM ER 3883
	2815	2				29	55	105		55	28	52	150																
	1816	2												66	61	58	35	120	32	35			79	89	27		26	KNM ER 3733
	2816	2				29	48	104		55	30	57	165																
	1817	2												64	57	59	29	122	26	27			72	83	28		24	OH5
	2817	2				36	45	107		60	31	55	146																
	1818	2												50	48	48	26	92	24	29			66	69	25		24	SES5
	2818	2				23	65	103		53	28	50	145																
	1819	2												50	47	47	25	97	25	28			62	69	22		24	NLD 37/38
	2819	2				26	60	93		47	24	48	135																
	1820	2												76	57	67	30	123					84	92	20		20	OH.9.
	2820	2				25	50	105		60	30	60																	

6/7/8/9 - END OF INFORMATION